

***Chromelosporium* re-evaluated, with *Chromelosporiopsis* gen. nov. and *Geohypha* stat. nov.**

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ABSTRACT—*Chromelosporium*-like asexual morphs of the subterranean *Pezizaceae* in the */Pachyphlodes* clade are not congeneric with the type of *Chromelosporium*. Some *Chromelosporium* morphs are of species in the */Pezizaceae* clade (the */Peziza* clade), and the genus *Chromelosporium* as it has been defined is polyphyletic. A diagnostic character that distinguishes these two groups is the presence or absence of conidiophore fasciculation. Mononematous conidiophores characterize *Chromelosporium* and species related to the */Peziza* clade. Synnematus conidiophores characterize *Pachyphlodes* and other asexual species and define the new genus *Chromelosporiopsis*, to be excluded from *Chromelosporium*. *Hyphelia terrestris*, long misapplied to *Chromelosporium*, is reevaluated, lectotypified, redescribed and recombined as *Geohypha terrestris*.

KEYWORDS—hyphomycete, nomenclature, taxonomy

Introduction

Collections of *Chromelosporium*-like hyphomycetes made by R.P. Korf around Ithaca, NY, which he tentatively named *Glischroderma* because of their production of gel (Korf 1994), were reevaluated by Healy & al. (2015) and identified as conidial morphs in the truffle genus *Pachyphlodes*. Fresh *Chromelosporium*-like specimens collected on bare soil in woods in Belgium, identified by DNA sequencing as *Pachyphlodes nemoralis* and *P. citrina*, provided the necessary asexual material to compare with and segregate from the asexually typified species, *Chromelosporium ochraceum* (Hennebert & Decock 2020).

The main distinction that emerged between the asexual morphs in *C. ochraceum* and the two *Pachyphlodes* species is conidiophore fasciculation. This criterion, applied to species already named in *Chromelosporium* (Hennebert 1973), segregates them into two genera. It seems generally accepted that these fungi are asexual morphs of *Pezizales*. As long as their type species are not known to be congeneric with species with a known sexual morph, however, it seems sensible to keep these genera separate.

Mononematous species define *Chromelosporium*. Synnematos species are excluded and are accommodated in the new genus *Chromelosporiopsis*.

Names such as *Botrytis epigaea*, *Phymatotrichum* species, and others are discussed as doubtful taxa. The conidial ornamentation observed in the numerous herbarium specimens that might contribute to the diagnosis of unidentified *Chromelosporiopsis* species is also analysed.

Hyphelia terrestris, currently misclassified in *Chromelosporium*, is re-evaluated and recombined as the type of *Geohypha* [= *Hyphelia* sect. *Geohypha* elevated to generic rank].

The asexual morph of *Plicaria endocarpoides*, previously supposed to show similarities with *Chromelosporium*, is described.

The illustrated descriptions of the asexual morphology of these taxa provide the rationale for the present paper.

Materials & methods

Species descriptions are based on observations made on herbarium material borrowed from many herbaria and some fresh collections made during 1960–62 while working as a postdoctoral researcher under the late Dr S.J. Hughes at the Agriculture & Agri-Food mycology group in Ottawa (DAOM). This material is complemented with some contemporary collections from Europe. A 1960 Olympus FH microscope equipped with Olympus positive low phase contrast objectives and an adapted Wild drawing tube was used for the microscopic examinations. All samples were mounted in lactic acid with Cotton blue. Slides made from the examined specimens are preserved in the Canadian National Mycological Herbarium, Ottawa, Canada (DAOM) and/or Mycothèque, Université Catholique de Louvain, Louvain-la-Neuve, Belgium (MUCL), and accession numbers are listed for each specimen in square brackets. Information provided in the Examined specimen sections duplicates the herbarium labels with bold numbers separating each specimen.

Taxonomy

Chromelosporium

This section includes the mononematous species considered morphologically congeneric with the type species *Chromelosporium ochraceum*, which currently

delimits the genus *Chromelosporium*. In addition, one *Peziza* and one *Plicaria* species with similar asexual morphs are each described.

Chromelosporium Corda, in Sturm's Deutschl. Fl., Abt. 3 (Pilze), 3(13): 81, 1833.

TYPE SPECIES: *Chromelosporium ochraceum* Corda??

Ascomycota, *Pezizaceae*, sexual morph unknown.

HYPHAE septate, creeping on the substratum.

CONIDIOPHORES mononematous, erect, septate, apically branching in successive symmetrical dichotomies, septate, apically obsuse.

CONIDIOGENUS CELLS subterminal and terminal branches forming synchronous conidia on denticles along their lengths, collapsing after rhexolytic secession of conidia.

CONIDIA holoblastic, one-celled, globose or subglobose, with wall ornamented from finely to coarsely verrucose, colored in mass.

HABITAT: on plant fragments.

COMMENTS—Hennebert (1973) made a clear distinction between *Chromelosporium* and *Ostracoderma* Fr., so *Chromelosporium* should not be placed as a synonym of *Ostracoderma* as cited in the 10th edition of Ainsworth & Bisby's Dictionary of the Fungi (Kirk & al. 2008) and in Index Fungorum. *Chromelosporium* is also incorrectly listed as a synonym of *Peziza* in Baral's contribution to Jaklitsch & al. (2016). Such synonymy is indeed impossible—*Peziza* being clearly polyphyletic and *Chromelosporium* an “orphan” genus. Pfister & al. (2016) did not mention the case when evaluating competing sexually and asexually typified names. Indeed, as the type species is not connected to any sexual morph, the generic name *Chromelosporium* cannot be competing so far. Also, *Chromelosporium* should not have been ignored in the recent “Outline” of fungal genera (Wijayawardene & al. 2020). It is possible that the four species described in the genus below, beside the type species, might also be revealed as polyphyletic.

Chromelosporium ochraceum Corda,

in Sturm's Deutschl. Fl., Abt. 3 (Pilze), 3(13): 81, 1833.

FIGS 1, 2

≡ *Sporotrichum ochraceum* (Corda) Sacc. Syll. Fung. 4: 105, 1886.

≡ *Ostracoderma ochraceum* (Corda) S. Hughes, Canad. J. Bot. 36: 792, 1958.

= *Botrytis dichotoma* Corda, Icon. Fung. 1: 18, 1837.

≡ *Campsotrichum dichotomum* (Corda) Bonord., Handb. Mykol.: 102, 1851.

= *Botrytis isabellina* Preuss, Linnaea 25: 75, 1852.

≡ *Ostracoderma isabellinum* (Preuss) S. Hughes, Canad. J. Bot. 36: 792, 1958.

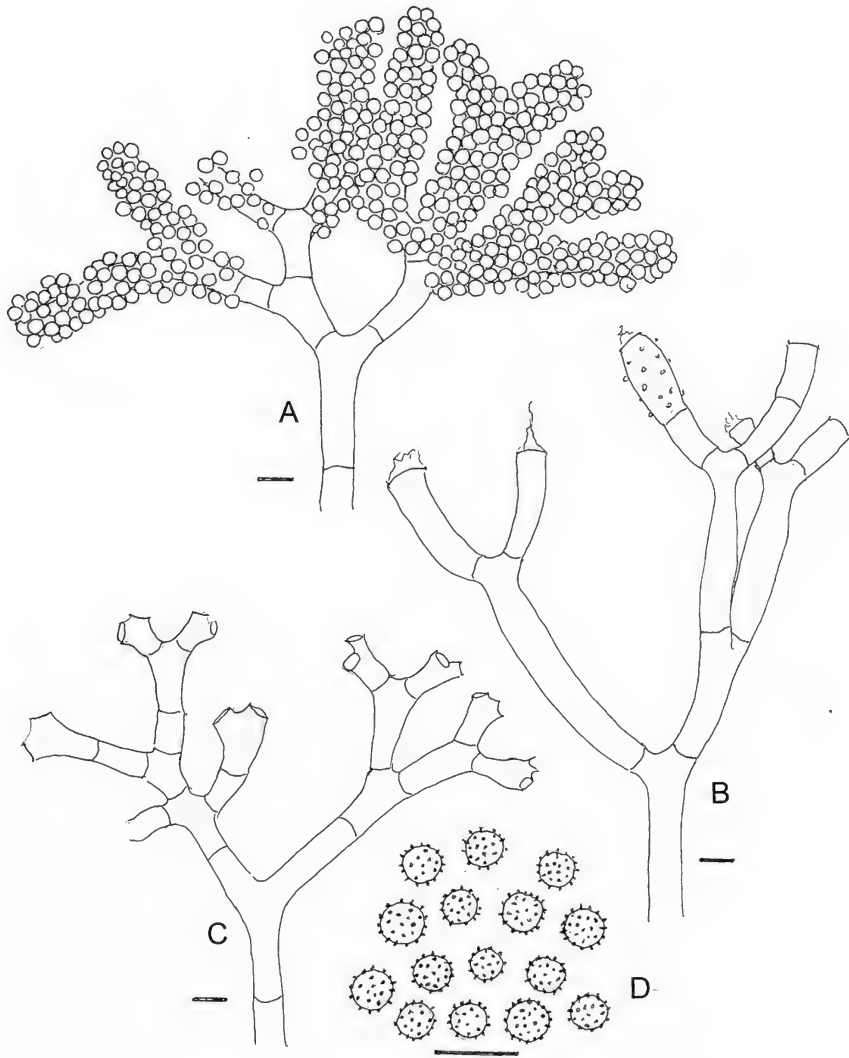


Fig. 1. *Chromelosporium ochraceum*. A. Conidiophore with conidiogenous cells (drawing by S.J. Hughes, DAOM 83330). B, D. Conidiophore and conidia (holotype, PRM 155414). C. conidiophore after secession of the conidiogenous cells (DAOM74695, Mycoth. Ven. 1080). Scale bar = 10 μ m.

= *Polyactis crystallina* Bonord., Abh. Naturf. Ges. Halle 8: 95, 1864.

= *Botrytis crystallina* (Bonord.) Sacc., Syll. Fung. 4: 135, 1886.

= *Botrytis spectabilis* Harz, Bull. Soc. Imp. Naturalistes Moscou 44(1): 144, 1871.

= *Clonostachys spectabilis* (Harz) Oudem. & Sacc., Ned. Kruid. Arch., 2. ser., 4: 539, 1886.

TYPE: *Chromelotrichum* [crossed out] *sporium ochraceum* Ca. *ramulis furcis*, *Myrinema generis*" [scr. et del. A.C.J. Corda]. On *Allium* dead stem, Prague, Czechoslovakia. Herb. Corda (Holotype: PRM 155414; isotypes: [DAOM 40946, MUCL.2895])

COLONIES in small patches, ≤ 10 mm diam., velvety, at first white, then ochraceous when mature.

HYPHAE 3–5 μm wide, creeping in the substratum.

CONIDIOPHORES mononematous, erect, emerging from hyphae in substratum, with a bulbous basal cell, $28\text{--}35 \times 12\text{--}15$ μm , ochraceous, extending into a cylindrical, septate stipe, $100\text{--}400$ μm long, pale ochraceous, the individual cells $40\text{--}95 \times 10\text{--}14$ μm , terminally repeatedly branched with up to five dichotomies, each branch with a basal septum and a second septum before the subsequent dichotomy, the length of branch decreasing from one dichotomy to the next, usually the first dichotomy $40\text{--}90 \times 9\text{--}10$ μm , the second $30\text{--}70 \times 6\text{--}10$ μm , the third $30\text{--}50 \times 6\text{--}9$ μm and so on, but in some cases dichotomies being very short decreasing from 20 to 10 μm , the angle of the dichotomies ranging from 30° to 45° .

CONIDIOGENOUS CELLS comprising the last four and five terminal dichotomies, together $70\text{--}100 \times 6\text{--}9$ μm , apically clavate, ≤ 11 μm , covered with synchronous conidia borne on a denticle, and collapsing after conidial release, seceding or (rarely) remaining as a frill on the last conidiophore cell.

CONIDIA holoblastic, borne simultaneously on denticles 2×1 μm , one-celled, globose or subglobose, ochraceous to salmon-colored in mass, $4\text{--}6.5$ μm , wall 0.5 μm thick, cyanophilic, verrucose, warts prominent 0.3 μm high and blunt, with 12–14 warts in median view, seceding rhexolytically.

HABITAT: on plant fragments.

DISTRIBUTION: Europe: Italy, France, Belgium, England, Africa: Maroc, Uganda, Asia: Sumatra.

COMMENTS—The name *Chromelosporium* remained unused until Hughes (1958) brought the genus to light. Corda's 1833 description of an overmature collection was so unclear that even Corda (1837) himself did not recognize the conspecificity of his later taxon, *Botrytis dichotoma*. His figure (FIG. 3A) shows globose ochraceous conidia accumulated along the sides and the top of the obtuse dichotomous branches.

Korf & Hennebert (1975) stated that *Botrytis spectabilis* was a synonym of *Chromelosporium ochraceum* based on an original illustration from Harz reproduced here (FIGS. 3B–C) and preserved in MUCL 1072.

The names *Botrytis spectabilis* and *Polyactis crystallina* (another synonym of *Chromelosporium ochraceum*) have been misapplied to the asexual morph

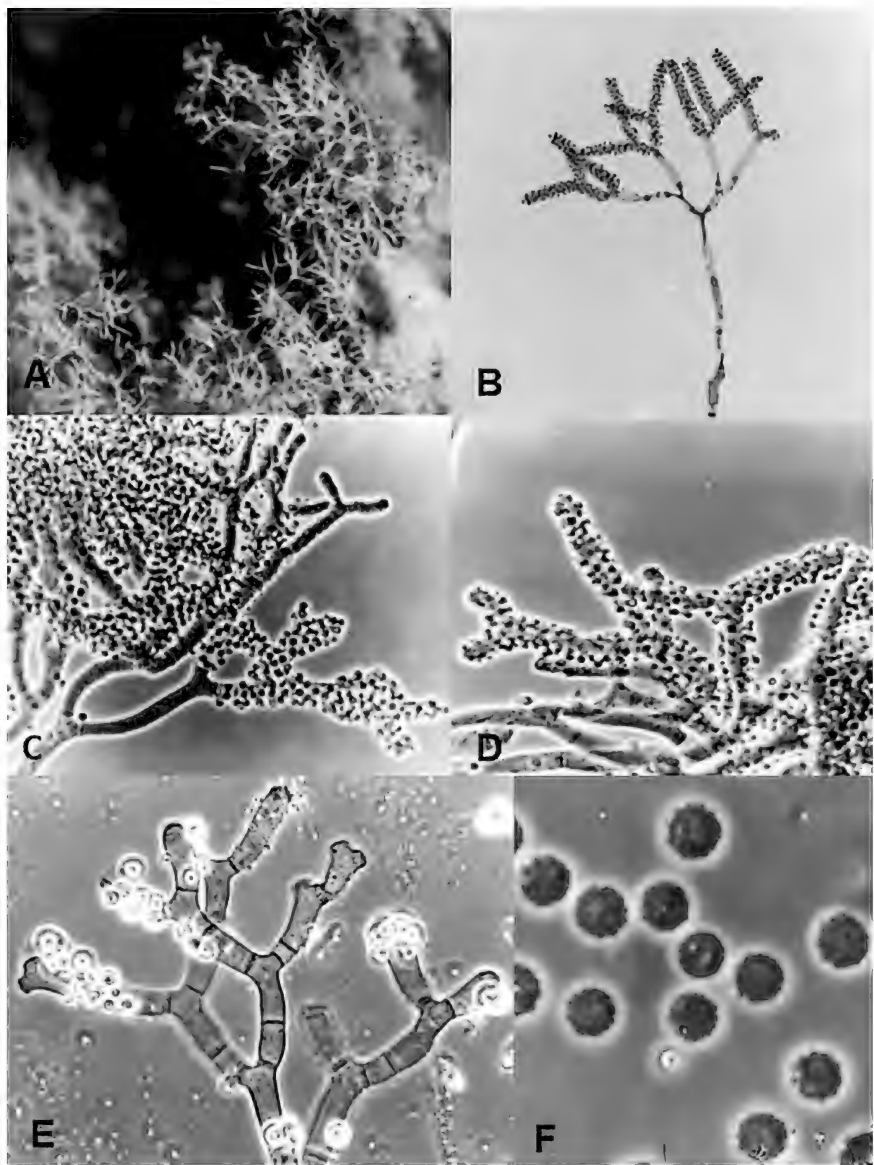


Fig. 2. *Chromelosporium ochraceum* (DAOM 46357). A. Conidiophores under low magnification. B. Dichotomies of conidiophore. C-D. Conidiogenous dichotomies. E. Conidiophore after secession of conidiogenous cells. F. Verrucose conidia.

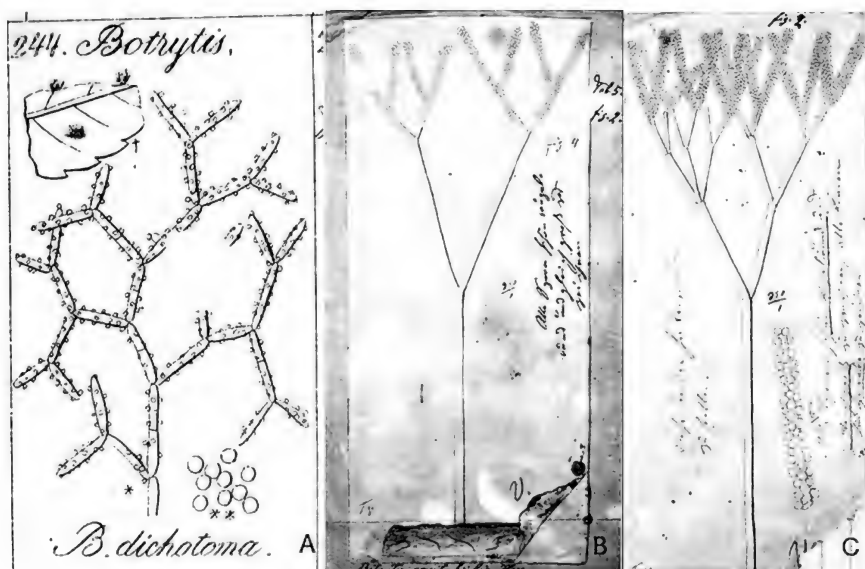


Fig. 3. Illustrations of A. *Botrytis dichotoma* Corda, Icon. Fung. 1: 18, fig. 244, 1837.
B-C. *Botrytis spectabilis* Harz, original drawings (MUCL 1072).

of *Peziza ostracoderma* Korf (Hennebert & Korf 1975). For that reason, both *Botrytis spectabilis* and *Polyactis crystallina* have been erroneously listed as synonyms of *Peziza ostracoderma* in Index Fungorum. *Chromelosporium ochraceum* is also erroneously cited as a synonym of *C. fulvum* (Link) McGinty & al., typified by the asexual morph of *Peziza ostracoderma* in Seifert & al. (2012, p. 139).

The lectotype collection of *Botrytis isabellina* and the authentic collection distributed in Rabenhorst's KLOTZSCHII HERBARIUM VIVUM MYCOLOGICUM N° 1570, were described in sufficient detail by Preuss (1853) as "Floccis erectis crassis repetito ramosis dichotomis vel trichotomis, apice verrucosis sporis irregulariter accumulatis, globosis, hilo instructo, episporio verrucoso" to confirm its synonymy with *Chromelosporium ochraceum*.

SPECIMENS EXAMINED

TYPE & AUTHENTIC MATERIAL. EUROPE: CZECHIA: (2) *Botrytis dichotoma*, Herb. Corda (PRM 155393 type), [DAOM 84706, MUCL 2896]. GERMANY: (3) *Botrytis isabellina* Preuss 1850, auf [rotten] nadelholz, Herb. Preuss 451 (B) (designated here as lectotype MBT 392406) [MUCL 5999]. (4) *Botrytis isabellina* Pr., ad lignum abietinum humi jacentem, prope Hoyerswerda [Germany], Preuss [1851],

Rabenh., Klotzschii Herb. Viv. Mycol. 1570 (B, PR, BM, BR, PAV, L) (isoelectotypes) [DAOM 51762, MUCL 1810]. (5) *Botrytis spectabilis* Harz, original drawing by Harz (isoelectotype 1975) (MUCL 1072).

OTHER SPECIMENS. **EUROPE: ITALY:** (6) *Botrytis epigaea* Link f. *ochracea* Sacc, ad terram argillosam in horto botanico, Padova. Aug. 1902. D. Saccardo, Mycotheca italica Mucedinaceae. [1903, Cent. XII] n° 1178 (PR 184863, BM, L 910.224-158) [DAOM 74898, MUCL 1803]. [The name has been listed in *Michelia* I :102, 1877]. (7) *Botrytis dichotoma* Corda, in sarmentis, foliis, capsulis putrescentibus, in Horto botanico ticinensi. Autumno, coll. Cavara. Micol. Lomb. n° 137, tab. 1, fig. 20-24 [1894]. Cavara, Fungi Longobardiae exsiccate. 195, (PAD, BM, PAV, BPI, NY, B, L) [DAOM 83330, MUCL 1801]. (8) *Botrytis fulva* Link. in scapis *Allii cepae*, Consiglio (Treviso). Sept. 1897. D. Saccardo Mycotheca italica Mucedinaceae. Cent. II.186, (K-M) [DAOM 74699, MUCL 1802]. (9) *Botrytis fulva* Lk. *Polyactis fulva* Bon. in truncis putridis. Selva (Treviso) Oct. 1876. Saccardo P.A. Mycotheca veneta. Cent. XI. 1897. n°1080 (K-M) [DAOM 74695, MUCL 1812]. (10) *Botrytis fulva* Link, ad corticem ramorum, Valtaro, Sept. 1923, coll. Renji, det. G. Bresadola, (BPI) [DAOM 83884, MUCL 2413]. (11) *Botrytis fulva* Link f. *argillacea*, ad *Salicem petandram*, Eichler, Polachia, 1894. [scr. Bresadola] Herb. Bresadola, [In Bresadola Fungi polonici a cl. Viro B. Eichler lecti. Ann. Mycol. 1, 2: 97-131, p. 127(1903), forma *argillacea* of *Botrytis fulva* Link is not described] (S) [MUCL2531]. **UK:** (16) *Botrytis fulva* Link. Queen's Cottage grounds, Kew, Nov. 1898. G.E. Massee. (K-M) [MUCL 2295]. (17) *Phymatotrichum*, on *Fagus sylvatica* rotten wood, Sheepleas, Horsley, Surrey, R.W.G. Dennis, March 2 1952. (K-M-IMI 49481) [MUCL 3547]. (18) *Botrytis splendida* Schwein., on mossy *Salix* bark, Wheatfen Broad, Norfolk, E.A. Ellis, (K-M-IMI 26983) [MUCL 3568]. (16) *Phymatotrichum*, on *Petasites ovalis*, Forge Valley, Yorkshire, coll. I.M.I., det. S.J. Hughes. (K-M-IMI 8160) [MUCL 3581]. (19) *Botrytis* (*Phymatotrichum*), on *Heracleum*, Forge Valley, Yorkshire, Sept. 16 1946, coll. I.M.I., det. S.J. Hughes. (K-M-IMI 6851) [MUCL3592]. (20) *Botrytis*, *Phymatotrichum*, on *Petasites* dead petioles, Forge Valley, Yorkshire, Oct. 1945, coll. I.M.I., det. S.J. Hughes, (K-M-IMI 1586) [MUCL 3595]. (21) *Phymatotrichum*, on *Eupatorium cannabinum*, Farwath, Newton Dale, Piking, Yorkshire, Aug. 6 1960, W. Bramley. (K-M-IMI 83016a) [MUCL 3622]. (22) *Phymatotrichum*, on *Heracleum*, Forge Valley, Yorkshire, Sept. 16 1946, coll. I.M.I., det. S.J. Hughes. (K-M-IMI 7341) [MUCL 3582]. **FRANCE:** (12) *Botrytis fulva* Link, in ligno putrido, Côte d'Or, Sept. 1889, coll Fautrey n°9 (PC) [DAOM 83390, MUCL 2378]. (13) *Botrytis fulva* Bon., sur tricot de coton pourri près d'un lavoir, Lyon, coll. J.J. Therry. Cryptogames du Lyonnais. J.J. Therry n° 6474, (G) [MUCL 2398]. (14) *Botrytis carnea* Schum., ad culmos Paludi, Meudon, Nov. 3 1893, coll. E. Roussel. (PC) [MUCL 2706]. **BELGIUM:** (23) *Phymatotrichum*, on herbaceous stems and leaves of compositae, Forêt de Soignes, Sept. 16 1956, coll. M.B. Ellis. (K-M-IMI 69956) [MUCL 3542].

AFRICA: MOROCCO: (24) *Phymatotrichum*, sur souche de *Quercus ilex*, Forêt d'Azrou, Moyen Atlas, Maroc, 17 Nov. 1965, G. Malençon. Herb. Cryptog. G. Malençon 5805, (PC) [MUCL 8041]. **UGANDA:** (25) *Botrytis*, on dead wood, Kampala, 4000', May 1936, G. Hansford. Herb. Mycol. Dep. Agric. Uganda n° 1769 (K-M-IMI 7899) [MUCL 3613].

ASIA: INDONESIA: (26). *Botrytis*? op aarde, bladeren, takjes, Sumatra, Kampong Baroe bij Medan, Juli 1927, K.B. Boedijn. n° 4619 (Bot. Museum Utrecht 179892) [MUCL 5381].

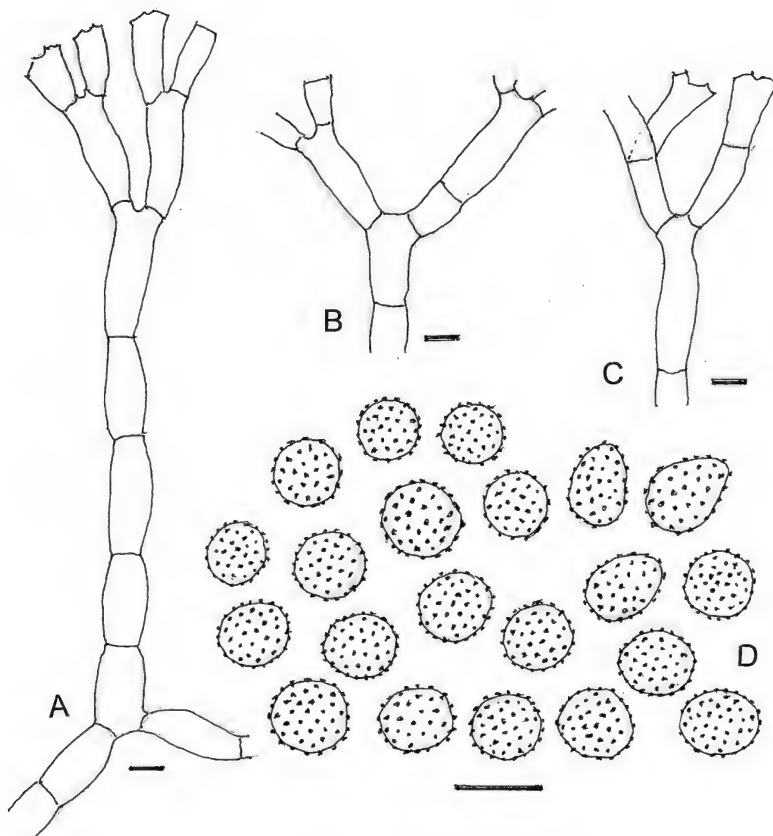


Fig. 4. *Chromelosporium herbicola* (isotype NY, MUCL 5889). A-C. Conidiophores missing the seceded conidiogenous cells. D. Verrucose conidia. Scale bar = 10 µm.

***Chromelosporium herbicola* (Ellis & Dearn.) Hennebert, comb. nov.**

FIG. 4

MB 833990

≡ *Rhinotrichum herbicola* Ellis & Dearn., Proc. Canad.

Inst., n.s. 1: 90, 1897 [(as "*herbicolum*").

TYPE: *Rhinotrichum herbiculum* E[llis] & Dearness, on *Solidago virga-aurea* golden rod stems, Aug. 13 1895, D.V.S. Valley, London, Canada, J. Dearness. Herb. Dearness 2314 (Holotype: DAOM [MUCL2321]; isotype NY [MUCL 5889]).

COLONIES in small patches, 3–5 mm wide, about 1 mm high, ochraceous.

HYPHAE 5–15 µm wide, creeping on the substratum.

CONIDIOPHORES mononematous, erect, emerging single from creeping hyphae, as a stipe 100–150 µm high, 9–15 µm wide, ochraceous, slightly constricted at septa in cells 25–35 µm long, terminally branching in successive dichotomies, at 10–45° angles, branches septate at the base and sometimes over their length, first dichotomies 30–50 µm long, second dichotomies 20–25 µm long,

CONIDIOGENUS CELLS presumably the third and fourth dichotomies collapsed and fallen away, not observed in the material but similar to those of *Chromelosporium fulvum* after Sumstine (1911).

CONIDIA presumably holoblastic, borne simultaneously all along the conidiogenous cell as described by the original authors, globose to obovate, one-celled, (6–)7–9(–11) µm, ochraceous, thick-walled and verrucose, with 18–20 warts in median view, seceding rhexolytically.

HABITAT: On decaying herbaceous plant stems, similar to *Solidago*.

DISTRIBUTION: Canada: Ontario.

COMMENTS – The original description of *Rhinotrichum herbicola* by Ellis & Dearnass reads: “Effuse, light yellow, becoming brown in the center. Hyphae coarse, septate, branched, nearly hyaline, 8–10 µ, thick, Fertile hyphae sub-undulate above, tips swollen and bearing the globose, sub-hyaline, finely echinulate, 7–9 µ, conidia. On dead stems of *Solidago canadensis*, London, Can., Aug. 1895. Herb. Dearnass n°2314.”

Sumstine (1911) examined the isotype specimen in NY and observed that the “spores clustered at the apex of the fertile branches” Although “the specimen proved to be poor”, he concluded that “it resembles in many respects *Botrytis fulva* Link.” This comment joined to the observed dichotomous branching and the verrucose globose conidia leads to transfer the species to *Chromelosporium*.

The species differs from *Chromelosporium ochraceum* by its shorter conidiophores and conidial size and ornamentation.

Chromelosporium canadense Hennebert, Persoonia 7: 196, 1973.

FIGS 5, 6

= *Rhinotrichum carneum* Ellis & Everh., J. Mycol. 1(7): 93, 1885

(non *Chromelosporium carneum* (Pers.) Hennebert

TYPE: *Chromelosporium canadense* Hennebert, on rotten wood in forest, Gatineau Park, Gatineau, Quebec, Canada, 25.11.1960, leg. S.J. Hughes & G.L. Hennebert, (Holotype: DAOM 71947; isotype: MUCL 1689).

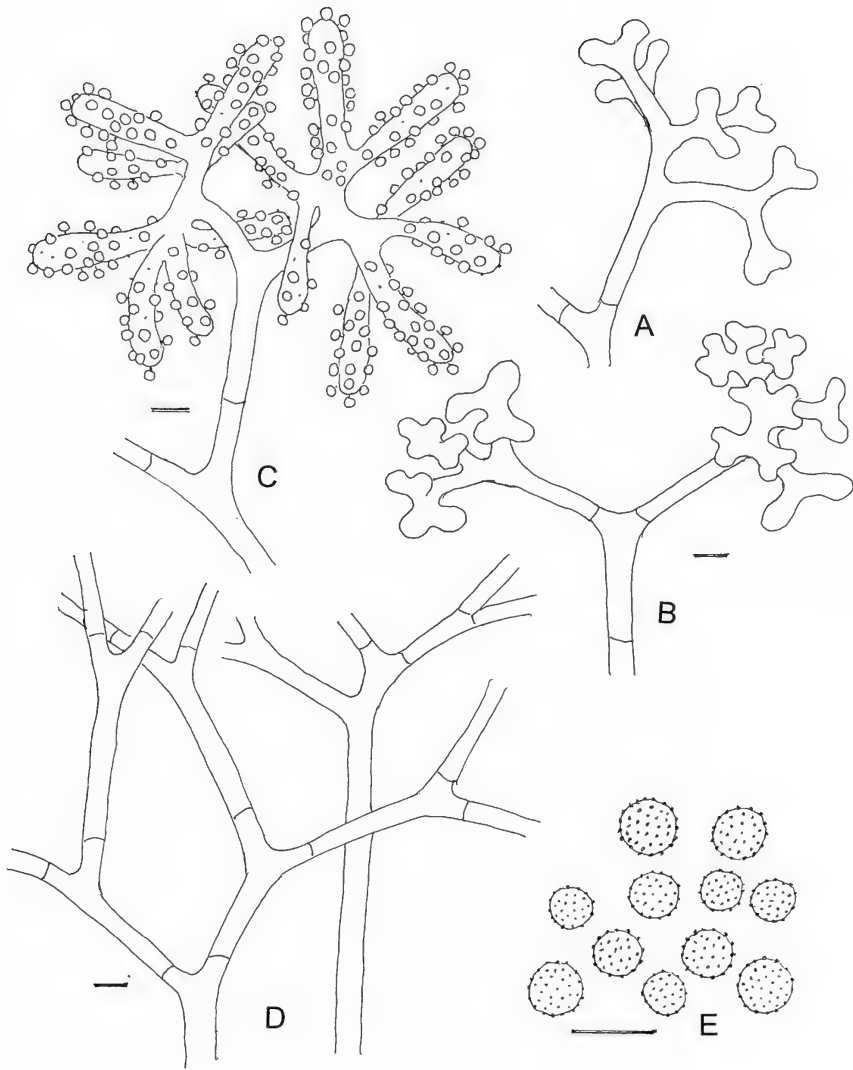


Fig. 5. *Chromelosporium canadense* (holotype, DAOM 71947). A. Young conidiogenous cells on terminal dichotomies. B. Primordia of the conidiogenous cells. C. Conidiogenous cells. D. Dichotomous branching of the conidiophore. E. Mature conidia. Scale bar = 10 µm.

COLONIES in patches ≤ 15 mm wide and ≤ 3 mm thick, effuse, loose, first white, then tawny to cinnamon, composed of mixed hyphae and branched conidiophores bearing clusters of conidia.

HYPHAE on substrate, thin, 4–7 μm , evanescent.

CONIDIOPHORES mononematous, erect, single, tawny, stipes 100–300 $\times$ 6–10 μm , then branching in regular and repeated dichotomies of different lengths, branches divergent at 20–60° angle, the basal ones 160–200 μm long, the distal ones shorter (16–48 μm), 10–12(–18) μm wide, the stipe and each branch septate at its base, the last dichotomy bearing two clusters of 4–8 primordial conidiogenous cells.

CONIDIOGENOUS CELLS formed as two groups of quadri-furcate terminal primordia that elongate up to 30–45 $\times$ 12–22 μm , slightly clavate, becoming conidiogenous over their entire length.

CONIDIA holoblastic, borne simultaneously on denticles, one-celled, globose, (3.5–)4–5(–7) μm , tawny, verrucose with 10–18 warts in median view, seceding rhexolytically.

HABITAT: on rotten wood and bark, branches, mosses, plant stems and herbs, in gardens and forests.

DISTRIBUTION: Canada and USA.

COMMENTS—Growth on PDA was obtained from young conidiophore hyphae taken after 3 days at 4°C from fresh material of four collections (MUCL 1689 T, 1690, 1691, 1692) but not from conidia. Mycelium in culture is effuse, ochre, forming dense dispersed patches; hyphae are regular, septate, branching at an angle of c. 45°, or very irregular, closely septate in swollen cells. In two cases, small clusters of dark brown cells were produced, suggesting primordia of apothecia.

Herbarium specimens often lack the conidiogenous cells which are collapsed or absent; their presence is inferred from the branching pattern and the conidial characters.

SPECIMENS EXAMINED:

TYPE & AUTHENTIC MATERIAL: **USA: OREGON:** (2) *Rhinotrichum carneum* Ell. & Ev., on bark, Oregon, 1885, W.S. Carpenter n° 125 [scr. Ellis] (NY). [DAOM 84659, MUCL 2694]. (holotype) **NEW YORK:** (3) *Rhinotrichum carneum* Ell. & Everh., on rotten wood, Macoun [scr. Ellis]. Ellis Collection (NY) [DAOM 84677, MUCL 2839]. (4) *Rhinotrichum carneum* Ell. & Everh. [no substrate, no date], Macoun [scr. J.B. Ellis]. Ellis Collection (NY) [MUCL 2840].

OTHER SPECIMENS: **CANADA, ONTARIO** (5) *Hyphelia terrestris*, on *Tilia*, Nashville, York Co., Oct. 25 1953, coll. det. R.F. Cain (TRT 30178) [DAOM 84684, MUCL 2858]. (6) *Hyphelia terrestris*, on hardwood, Nashville, Nov. 14 1954, coll.

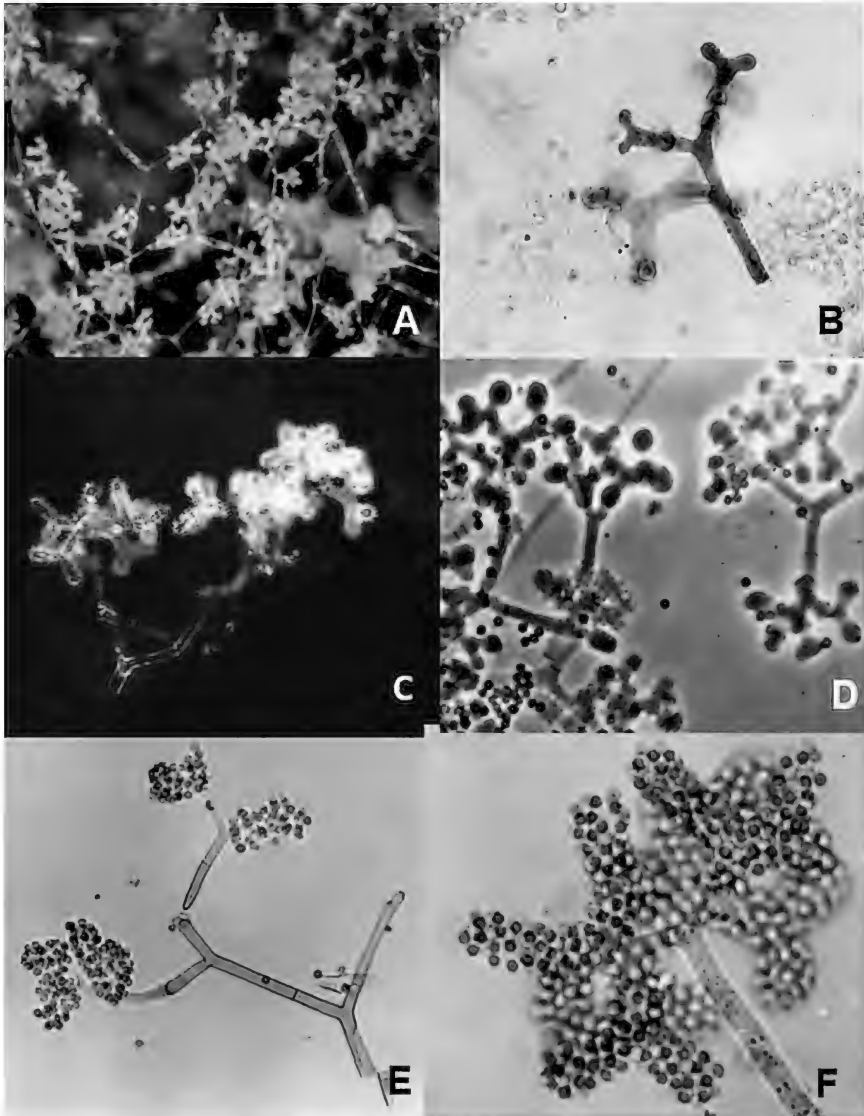


Fig. 6. *Chromelosporium canadense* (holotype, DAOM 71947). A. Conidiophores at low magnification. B-D. Young stages of conidiogenous cells. C. Half and fully mature conidioma. E. Wide angle of the dichotomies. F. Terminal bunch of mature conidiogenous cells.

det. R.F. Cain (TRT 31311) [DAOM 84683, MUCL 2857]. (7) *Hyphelia terrestris*, on *Populus* Nashville, Oct. 22 1955, coll. det. R.F. Cain (TRT 31699, BPI) [MUCL 2419]. (8) *Hyphelia terrestris*, on decayed log, New Durham, Brant Co., Oct. 14 1956 (TRT

32870) [DAOM 84688, MUCL 2862]. (9) *Botrytis fulva* Link, on dead wood, Oct. 20 1896, Macoun [Scr. J.B. Ellis]. Herb. Ellis (BPI) [DAOM 83886, MUCL 2415]. (10) *Botrytis (Phymatotrichum) fulva* Link, on decayed wood, N. Bathurst street Toronto, Nov. 17 1934, H.S. Jackson, det. D.H. Linder, Herb. R.F. Cain 8207 (TRT 8065, FH, DAOM 81409) [MUCL 2889]. (11) *Botrytis (Phymatotrichum) fulva* Link, on rotten wood, S. Aurora, Oct. 23 1932, H.S. Jackson, det. D.H. Linder. Herb. R.F. Cain 8210 (TRT 8060, DAOM 81410) [MUCL 2890]. (12) *Ostracoderma*, on soil of lawn, North Toronto, June 17 1960, S.J. Hughes. (DAOM 83325) [MUCL 2255]. (13) *Chromelosporium*, on bark and plant decay, South March, April 10 1962, G.L. Hennebert (MUCL 3067). **QUÉBEC** (14) *Ostracoderma* on bark, Gatineau Park, Nov. 25 1960, S.J. Hughes. (DAOM 71946) [MUCL 1688]. (15) *Ostracoderma*, on wood, Gatineau Park, Nov. 25 1960, S.J. Hughes. (DAOM 71948) [MUCL 1690]. (16) *Ostracoderma*, on wood, Gatineau Park, Nov. 25, 1960, S.J. Hughes. (DAOM 71949) [MUCL 1691]. (17) *Ostracoderma*, on wood, Gatineau Park, Nov. 25, 1960, S.J. Hughes. (DAOM 71950) [MUCL 1692]. (18) *Ostracoderma*, on wood and bark, Gatineau Park, Oct. 31, 1960, S.J. Hughes. (DAOM 71399) [MUCL 1689]. (19) *Ostracoderma*, on stem of *Veratrum viride*, Yoho Valley, Aug. 8 1960, S.J. Hughes. (DAOM 71326) [MUCL 1513]. (20) *Chromelosporium*, on *Betula papyrifera* rotten wood, Gatineau Park, Oct. 31 1960, G.L. Hennebert. (DAOM 71545, MUCL 1590). (21) *Chromelosporium*, on rotten wood, Gatineau Park, Oct. 7 1960, G.L. Hennebert. (DAOM 71419, MUCL 1505). **MANITOBA** (22) *Botrytis* near *phymatotricha* Sacc. prov. cfr. *lateritia*, C.E. Fairman suggests *Botrytis carnea* Schum, on old board, Winnipeg, Sept. 16 1928, G.R. Bisby 4140 [scr. Dearness]. Herb. Dearness 6732 (DAOM 84789) [MUCL 3070]. **USA, OHIO** (23) Mycobiota of Ohio. *Botrytis isabellina* Preuss, on rotten wood, The 7 Caves, Highland Co., coll. det. D.H. Linder 2667, Sept. 6 1933, Herb. W. Bridge Cooke (NY, FH, DAOM 84679) [MUCL 2847]. **IOWA** (24) *Hyphelia laxa* Schw., on decorticated conifer wood. (IA) [DAOM 83317, MUCL 2260]. **SOUTH CAROLINA:** (25) *Botrytis epigaea* Link var. on clay surface after rain, Sept. 1883, H.W.R. [scr. H.W. Ravenel]. Herb. U.W. Ravenel, (K-M, DAOM 83332) [MUCL 2281]. **MASSACHUSETTS** (26) *Botrytis?* *Hyphelia spectabilis* Harz, on coniferous bark, York, Sept. 14 1891. Herb. Thaxter 137 (FH) [DAOM 84702, MUCL 2886]. (27) *Botrytis fulva* Link, on hardwood branches on the ground, Beaver Brook reserve, Belmont, Oct. 3 1937, coll. G.D. Darker 64-90, det. D.H. Linder. (FH) [DAOM 84703, MUCL 2888]. **NEW YORK** (28) *Ostracoderma canadense*, on stem of fern in a pond, Forest Home, Ithaca, May 1 1962, G.L. Hennebert. (MUCL 3120). **NEW JERSEY** (29) *Botrytis epigaea* Pers., on old pine boards partly buried in the ground, Newfield, N.J., Sept. 1881, Ellis. Ellis North American Fungi 827 (WIS, CUP, K-M, B, G, L) [MUCL 1804].

Chromelosporium arenosum Hennebert, Persoonia 7: 196, 1973.

FIG. 7

TYPE: Flora Venezuelae 2474, on rotten wood of *Espeletia*, 3550 m, alt., Mucudaji, Sanide Santo Domingo, Estada Mesida, July 22 1958, coll. R.W.G. Dennis. (K-M) (Holotype: MUCL 2298 [DAOM 83359]; isotype IMI 75582 [MUCL 5889]).

ETYMOLOGY: from the Latin *arenosus* or sand-like, suggesting the spreading granulose aspect of the sporulating conidiophores of ochraceous color seen under low magnification.

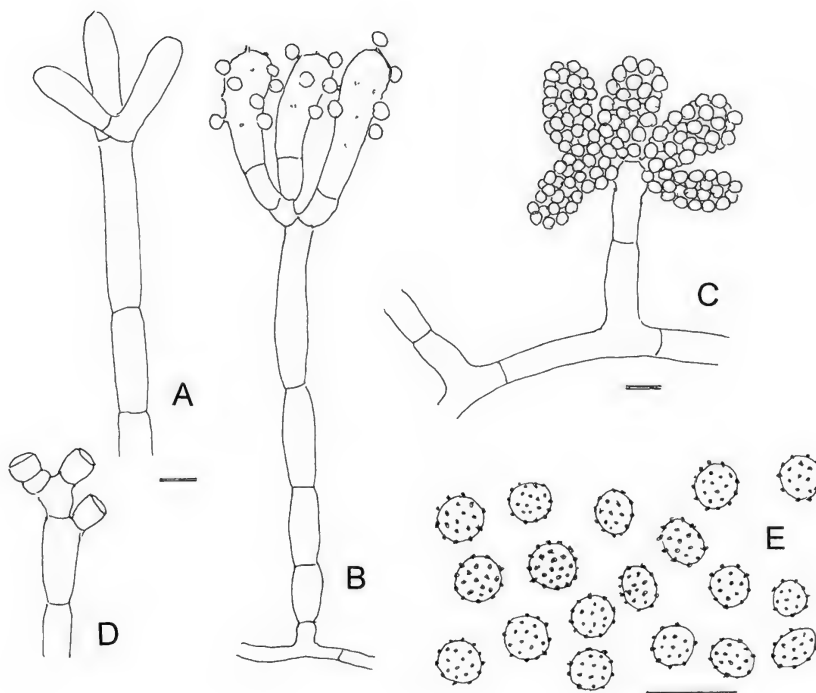


Fig. 7. *Chromelosporium arenosum* (holotype, DAOM 83359). A. Young conidiophore branching. B. Erect conidiophore with conidiogenous cells. C. Mature conidiophore with conidia borne on aerial hypha. D. Conidiophore after secession of conidiogenous cells. E. Conidia. Scale bar = 10 µm.

COLONIES superficial, sparse, delicate, cobweb-like white mycelium, becoming arenose ochraceous with mature conidiophores appearing like minute, scattered grain.

HYPHAE repent, hyaline, single, 7–9 µm wide, regular, straight, branched, thin-walled, smooth, septate with cells 7–12 µm long, sometimes regenerating after collapse from septum by internal narrow hyphal proliferations 3–4 µm wide.

CONIDIOPHORES arising singly, mononematous, as erect branches of the repent hyphae, short, 70–100 µm high, 8–9 µm wide, stipes with the basal cell bulbous 11–13 × 6–8 µm, constricted at septa, cells 15–50 µm, apically branching in dich- or trichotomies forming 2–8 terminal cells 40–50 µm long, obtuse, clavate up to 13 µm wide and conidiogenous.

CONIDIA holoblastic, borne simultaneously on denticle $1 \times 0.5 \mu\text{m}$, one-celled, globose or ovoid, $3.5\text{--}5.5 \times 3.5\text{--}6.5\text{--}(8.1) \mu\text{m}$, mostly $4.5 \mu\text{m}$ wide, $0.5\text{--}1 \mu\text{m}$ thick-walled, the outer wall hyaline, the inner wall subhyaline to ochraceous and coarsely verrucose, with 6–10 globoid or elongate warts in median view, seceding rhexolytically.

HABITAT: on rotten bark of *Espeletia* sp. in the Tropics.

DISTRIBUTION: Venezuela.

Chromelosporium macrospermum Hennebert, Persoonia 7: 197, 1973. FIG. 8

TYPE: living and dried cultures from *Peziza* sp. ind. on sterilized soil in greenhouse, Heverlee, Belgium, 2.04.1960, leg. G.L. Hennebert (Holotype: MUCL 1116; isotype DAOM 67492 = dried culture of MUCL 1116).

COLONIES on malt agar substrate thin, white to rust-color when sporulating, comprising interwoven and prostrate hyphae, hyaline to subhyaline, producing laterally large spherical cells, $40\text{--}50 \mu\text{m}$ diam, thin-walled.

CONIDIOPHORES mononematous, erect, pale to rust-colored, septate, stipes $400\text{--}600 \times 15\text{--}18 \mu\text{m}$, apically bi- or quadri-furcate, branches $20 \mu\text{m}$ long, few septate, the distal ones erect, radiate, cylindrical to clavate $130\text{--}160 \times 20\text{--}25 \mu\text{m}$, conidiogenous.

CONIDIA holoblastic, borne on a denticle, more or less simultaneous, globose, rust-colored, $15\text{--}23$ (av. 19.7) μm , thin-walled, finely punctate, seceding rhexolytically.

HABITAT: sterilized greenhouse or nature soil

DISTRIBUTION: Europe: Belgium, Oceania: Australia.

COMMENTS – This unique strain MUCL 1116 was found in one ascospore germinating from several apothecia then identified as *Peziza ostracoderma*, collected in a tropical greenhouse of the Faculty of Agronomy UCL in Heverlee, Belgium in 1960. Korf differentiated the size and ornamentation of the ascospores preserved in lactic acid mounted slides of the original *Peziza* apothecia (Hennebert & Korf 1975) but in the absence of the single original apothecium, he could not circumscribe the species. The same species has been isolated from soil in South Australia by Dr. G.C. Hansford at the University of Adelaide in 1953 and preserved as living culture IMI 54710 in the culture collection at Egham and as dried culture in K-M–IMI 54710 under the name *Phymatotrichum* tax. sp. 7. The culture is *C. macrospermum* mixed with conidia of *P. ostracoderma* and unidentified hyaline chlamydospores.

The species might be a mutant *Peziza ostracoderma* or a distinct undetermined species of *Peziza*.

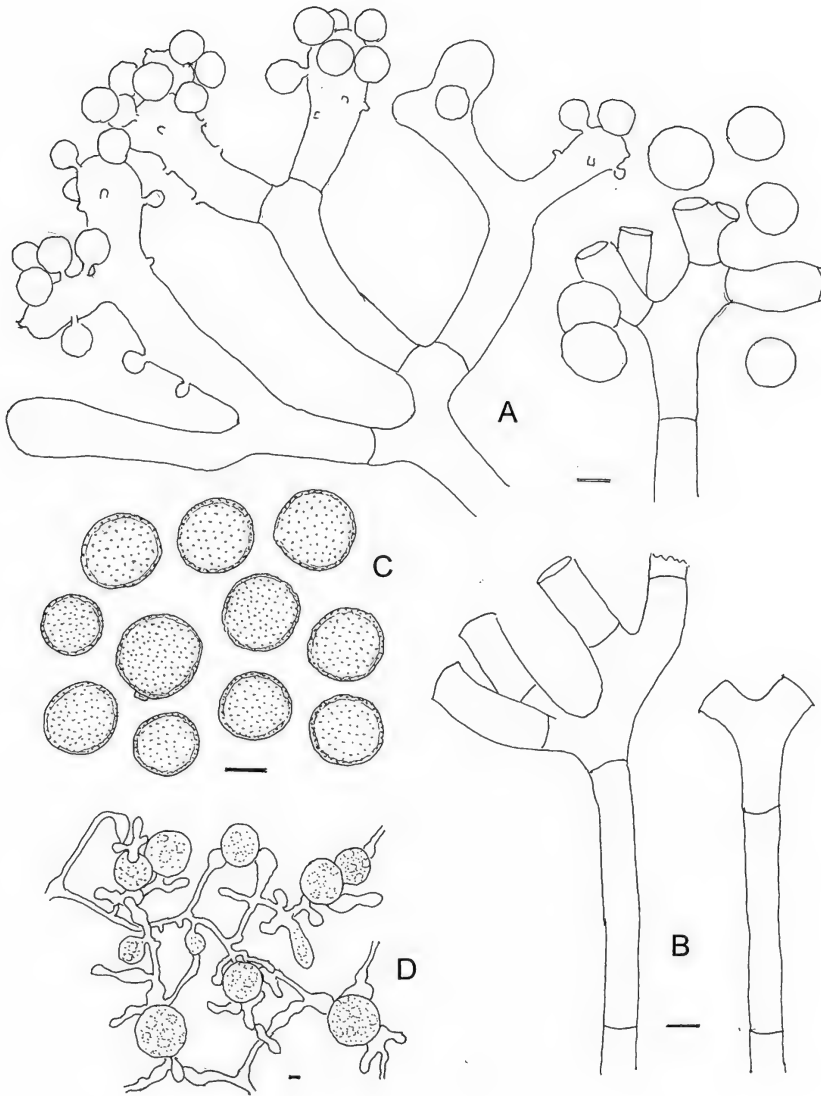


Fig. 8. *Chromelosporium macrospermum* (ex holotype, MUCL 1116). A-B. Conidiophores at diverse stages. B. Punctate conidia. D. Swollen cells in culture. Scale bar = 10 μ m.

Species of *Pezizaceae* with known sexual morphs and similar mononematous conidiophores and conidiogenesis

Peziza ostracoderma Korf, Mycologia 52: 650, 1961 ["1960"].

FIG. 9

- ≡ *Plicaria fulva* R. Schneid., Zentralbl. Bakteriол. Parasitenk. Infektionskrankh. Hyg., 2. Abt., 108: 147, 1954 [non *Peziza fulva* Pers. 1822, nom. sanct.].
- = *Dematium ollare* Pers., Syn. Meth. Fung. 2: 697, 1801.
- ≡ *Botrytis fulva* Link, Spec. Plant., ed. 4, 6(1): 58, 1824, nom. illeg. [superfluous].
- ≡ *Sporotrichum fulvum* Fr., Syst. Mycol. 3: 418, 1832, nom. sanct. [not "(Link) Fr."; non Link 1809].
- ≡ *Trichosporum fulvum* (Fr.) Fr., Summa Veg. Scand. 2: 492, 1849.
- ≡ *Polyactis fulva* (Fr.) Bonord., Handb. Mykol.: 115, 1851 [not "(Link) Bonord."].
- ≡ *Chromelosporium fulvum* (Fr.) McGinty, Hennebert & Korf, Mycologia 67: 216, 1975 [not "(Link) McGinty et al."].
- ≡ *Chromelosporium ollare* (Pers.) Hennebert, Persoonia 7: 197, 1973.
- = *Haplaria nitens* Delacr., Bull. Soc. Mycol. France 6: 140, 1890.
- = *Botrytis luteobrunnea* Krzemien. & Badura, Acta Soc. Bot. Poloniae 23: 727, 1955 (1954).
- = *Mycotypha dichotoma* F.A. Wolf, J. Elisha Mitchell Sci. Soc. 71: 217, 1955.
- ≡ *Ostracoderma dichotomum* (F.A. Wolf) Matsush., Icon. Microfung. Matsush. Lect.: 103, 1975.

TYPES: *Plicaria fulva* R. Schneid., on damp sterilized soil in greenhouse, Berlin-Dahlem, Germany, 25.3.1953 (Holotype: B; authentic material in CUP R.P.K. 4114).

Dematium ollare Pers.: dried culture from living culture of *Plicaria fulva* R. Schneider, on damp sterilized soil, greenhouse, Berlin-Dahlem, Germany, March 1953, received in Febr. 1954 from R. Schneider (Neotype: MUCL 1112, designated in Hennebert 1973; isoneotypes: dried culture DAOM 81809, living cultures CBS 382.54, CCRC 36608, IMI 059206).

COLONIES velvety to floccose, white when young, yellow to fulvous or cinnamon when sporulating, rapidly growing.

HYPHAE mostly prostrate, interwoven, branched, septate, anastomosing, hyaline to pale fulvous.

CONIDIOPHORES mononematous, solitary or gregarious, erect and divergent, arising from prostrate or aerial hyphae; stipe 130–600 × 8–17 µm, hyaline to fulvous, sparsely septate, attenuate at the base, apically 1–3 times dichotomously branched, dichotomies short, 10–25 × 5–13 µm, septate at the base, the terminal ones clavate, slightly inflated ≤15 µm, conidiogenous.

CONIDIOGENOUS CELLS producing conidia along their length, collapsing after release and seceding away at basal septa, leaving the stipe or the lowest dichotomies as a stump.

CONIDIA holoblastic, borne simultaneously on a denticle 3 × 1 µm, densely and irregularly spaced, globose or napiform, 5–9(–14) µm (mean = 7.5 µm), fulvous, wall thin, finely punctate, seceding rhexolytically. Conidia

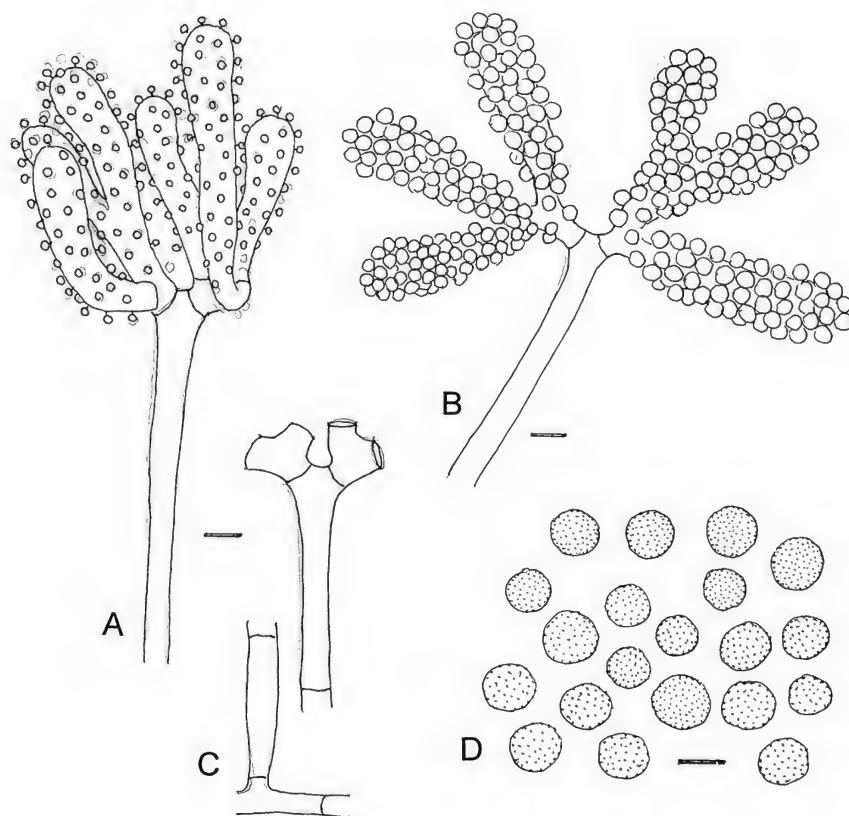


Fig. 9. *Peziza ostracoderma* (neotype MUCL 1112). A-C. Conidiophores at diverse stages. D. Punctate conidia. Scale bar = 10 μ m. The magnification of the line-drawings of conidia in figures 8 and 9 is half that in other figures.

germinate and colonies sporulate profusely on malt agar and diverse organic poor culture media.

HABITAT: On sterilized soil in greenhouses, on mushroom beds, on cardboard, paper pots, paper, and old textiles in moist chambers, on humid plaster walls in houses, on moist hay, on dung of rodents, and on forest soil.

DISTRIBUTION: Europe, North America, Asia.

COMMENTS—Korf (1961) knew the species in both its asexual and sexual morphs in the greenhouses at Cornell when he received the type and a living culture of *Plicaria fulva*. The species has elliptical ascospores like most *Peziza* species. Seeing the sanctioned name *Peziza fulva* Pers., he created the new

name *Peziza ostracoderma*, referring to Hughes' opinion that the conidial morph could be referred to *Ostracoderma*. Hennebert (1960) reported and described the same fungus observed in a tropical greenhouse of the Faculty of Agronomy UCL in Heverlee, Belgium, in 1960.

Hennebert (1973) segregated *Chromelosporium* from *Ostracoderma*, which Hughes (1958) had considered synonymous. He named the conidial morph of *P. ostracoderma*, *Chromelosporium ollare*, with *Dematium ollare* as basionym, which he neotypified with GLH 1112 (MUCL 1112) in the absence of an original authentic specimen from Persoon.

Hennebert & Korf (1975) cited *Dematium ollare* as the earliest post-Linnean name for the conidial morph common in greenhouses. Link (1824) transferred the species to *Botrytis* as *Botrytis fulva*, an illegitimate name with *Dematium ollare* cited as its unique synonym. Fries (1932a) excluded *D. ollare* from his genus *Dematium*, treating it, after Link, as a synonym of *B. fulva*, both of which he transferred into *Sporotrichum* as *S. fulvum*, a sanctioned name.

Searching for the earliest possible name to combine in *Peziza* in accordance with the 2017 Shenzhen ICN, it is apparent that the earliest name of the fungus, *Dematium ollare*, cannot be used, because of *Peziza ollaris* Fr. (Fries 1822), a different species, the name of which is sanctioned over *Peziza ollaris* Schaeff. (*Fungorum in Bavaria et Palatinatu circa Ratisbonam Icones* 4:126, 1774) and *Peziza ollaris* Pers. (*Mycol. Eur.* 1: 299, 1822), which might be the present species.

Despite what is posted on Index Fungorum, the names *Alytosporium fulvum* (Link) Link and *Nodulisporium fulvum* S. Hughes, being based on *Sporotrichum fulvum* Link, are synonymous with neither *Dematium ollare* nor *Botrytis fulva*.

Haplaria nitens, added here as a synonym, was collected on sterilized oak barks from a tannery used as mulch in a warm glasshouse of the Laboratoire de Pathologie végétale de l'Institut national Agronomique in Paris. Its conidia are minutely verrucose.

The variable conidiophore length and variable number and length of the dichotomies of the species might explain its frequent confusion with *Chromelosporium ochraceum*. The primary diagnostic differences reside in conidial size and ornamentation and the ecological habitat.

In an attempt to clarify the relationship with *Chromelosporium macrospermum*, the variability of conidial size in monoascospore strains of *Peziza ostracoderma* was studied on different culture media (malt-agar,

potato-dextrose-agar, carrot-agar, and jiffy-agar, a mixture of soil and peat). Although conidial size varied between 5–9 µm and one strain produced conidia ≤12 µm and a different strain produced conidia ≤14 µm, none reached 15–23 µm, the conidial size reported for *C. macrospermum* of.

TYPE SPECIMEN EXAMINED. EUROPE: FRANCE: (2). *Haplaria nitens* Del. n. sp. Paris (scr. Delacroix). (holotype, PC) [isotypes, DAOM 59453, MUCL2700]

OTHER SPECIMENS EXAMINED See Hennebert & Korf (1975).

Plicaria trachycarpa (Curr.) Boud.,

Hist. Class. Discom. Eur. 50, 1907, **var. *trachycarpa*** Figs 10, 11

≡ *Peziza trachycarpa* Curr., Trans. Linn. Soc. London 24: 493, 1864.

≡ *Discina trachycarpa* (Curr.) P. Karst., Acta Soc. Fauna Fl. Fenn. 2(6): 113, 1885.

≡ *Detonia trachycarpa* (Curr.) Sacc., Syll. Fung. 8: 105, 1889.

≡ *Curreyella trachycarpa* (Curr.) Massee, Brit. Fung.-Fl. 4: 401, 1895.

≡ *Lamprospora trachycarpa* (Curr.) Seaver, Mycologia 6: 19, 1914.

≡ *Plicariella trachycarpa* (Curr.) Velen., Monogr. Discomyc. Bohem.: 342, 1934.

≡ *Galactinia trachycarpa* (Curr.) Le Gal, Bull. Trimestriel

Soc. Mycol. France 78: 212, 1962.

= *Rhinotrichum trachycarpum* F.A. Wolf, J. Elisha Mitchell Sci. Soc. 74: 166, 1958.

= *Chromelosporium trachycarpum* Hennebert, Persoonia 7: 197, 1973.

TYPES: *Peziza trachycarpa* Curr., supra solum deustum, Ascot com. Surrey, Nov. 1862 (Holotype: K(M) 29980).

Chromelosporium trachycarpum Hennebert, asexual morph of *Peziza trachycarpa*, on burned area, Camp II, Allegany State Park, USA: June 11, 1961, coll. & isol. G.L. Hennebert, det. R.P. Korf (Holotype, DAOM 83324; isotype, MUCL 2197).

COLONIES fast growing on malt agar medium, pellicular, white to pale ochraceous.

HYPHAE thin, hyaline, interwoven and prostrate.

CONIDIOPHORES mononematous, erect, very short, 50–100 × 8–10 µm, repeatedly dichotomously or assymmetrically branched, irregularly septate, branches cylindrical, short, 20–35 × 8–10 µm, widely divaricate, becoming totally conidiogenous, forming compact globose conidial heads.

CONIDIA holoblastic, borne simultaneously on denticle, yellow-ocher, one-celled, globose or shortly ovate, 5–7 × 5–9 µm, wall finely verrucose, with 10–15 warts in median view, seceding rhexolytically.

HABITAT: in moist burned area in forests.

DISTRIBUTION: Northern Hemisphere.

COMMENTS—The drawings were made while I was in Canada from an ascospore culture of the species collected in Ontario (MUCL 2339) identified

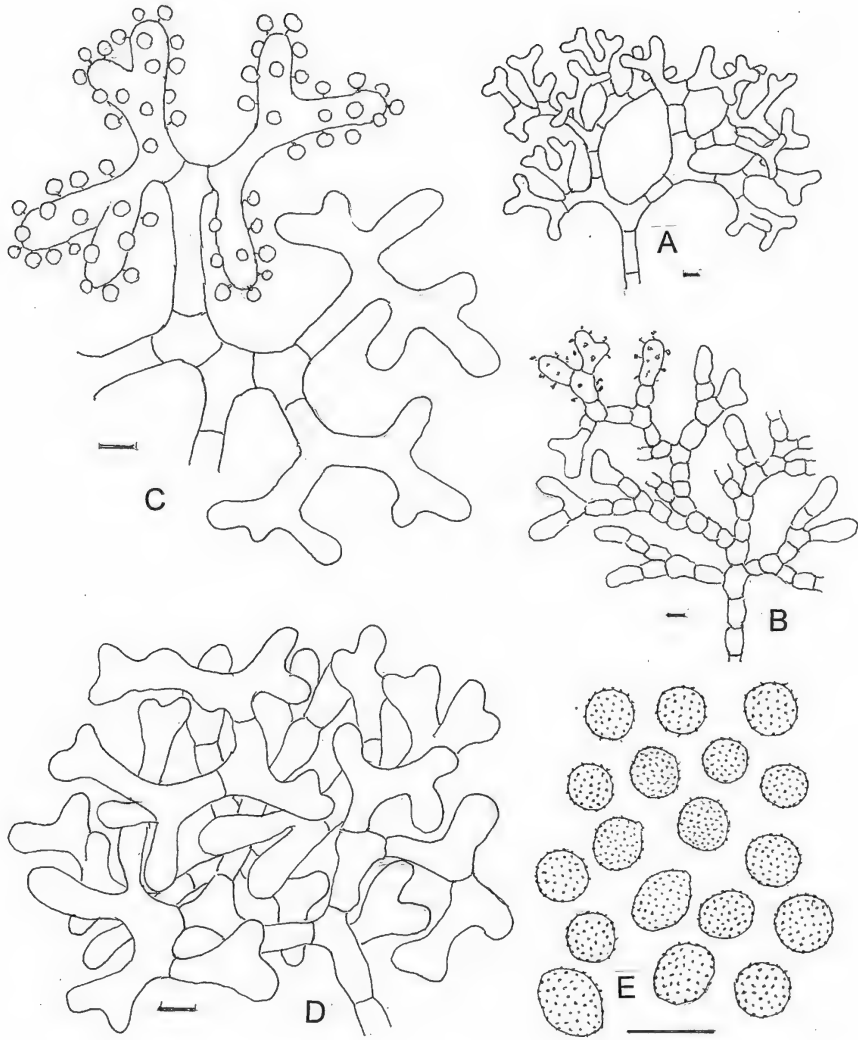


Fig. 10. *Plicaria trachycarpa*. A-B. Branched conidiophore. C. Terminal conidiogenous cells. D. Much septate conidiophore on porcine dung (MUCL 2933). E. Punctate conidia. (A-C and E on malt agar MUCL 2339). Scale bar = 10 μm.

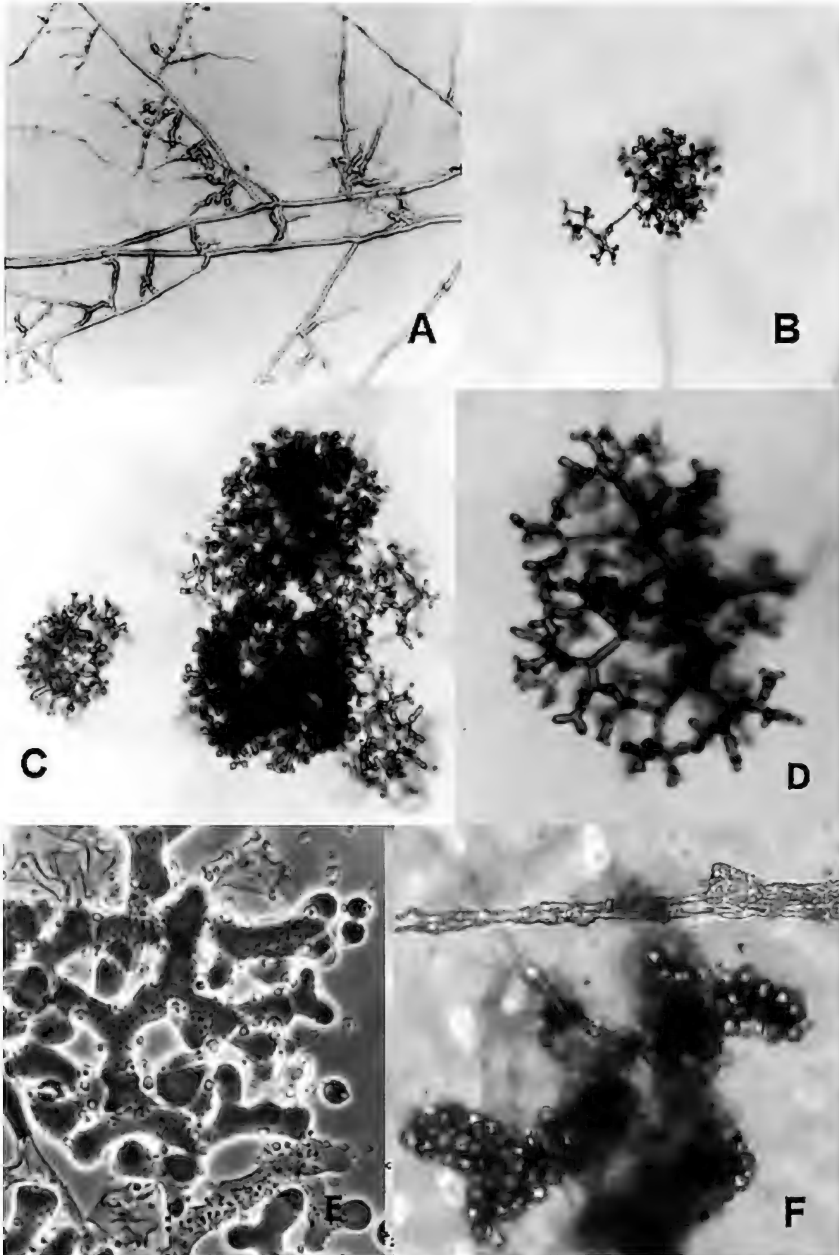


Fig. 11. *Peziza trachycarpa*. A. Initiation of conidiophores. B-D. Globular branched conidiophores showing the dichotomies. E. Initiation of conidia. (A-E, MUCL 2339). F. Mature conidiogenous cells (DAOMC 199631 = MUCL 57201 on malt-agar).

as identical to DAOM 83324 but not after examination of K(M) 29980. A living strain labelled as *Plicaria trachyspora* var. *muricata* (= *Plicaria carbonaria* (Fuckel) Fuckel 1870) was recently received as DAOMC 199631 that, on 2 % malt agar, developed similar clusters of dichotomous branches close to the substrate and bearing mature conidia.

SPECIMENS EXAMINED;

NORTH AMERICA: USA, NEW YORK (2) *Peziza trachycarpa* Currey, on burned area, State Line Run, near Onoville, Cattarangu Co., June 10 1961, coll. Kumi T Korf, det. R.P. Korf (MUCL 2198). (3) *Chromelosporium*, on porcupine dung (in moist chamber) from Stoddard Brook Road, Allegany State Park, June 11 1961, coll. & isol. G.L. Hennebert. (DAOM 89363, MUCL 2933). **CANADA, ONTARIO** (4) *Peziza trachycarpa* Currey, on moist clay soil in mixed woods, Bell's Corners, July 31 1961, coll. & isol. G.L. Hennebert 2339. (DAOM 83382, MUCL 2339). (5) *Plicaria trachycarpa* (Currey) Boudier var. *muricata* Grelet on burned litter in burned mixed forest, Renfrew Co., Ont., Sept. 2 1979, K.N. Egger 0281, dried and culture (CCF 6918, DAOMC 199631, MUCL 57201).

EUROPE: UK (6) *Peziza trachycarpa* (Curr.) Boud., conidia on cardboard flower pot., Evesham, Worcs., March 25 1955, col. R.E. Taylor, det. R.W.G. Dennis. Dried culture IMI 59800) [MUCL 3514].

Chromelosporiopsis

Chromelosporium-like species with synnematus conidiomata resemble mononematous *Chromelosporium* species in having the same conidiogenesis and ornamented globose conidia but differ in the conidiophore fasciculation and asymmetric sparsely septate dichotomous branching (a branching pattern described here as coralloid). This concerns two asexual species named by Hennebert (1973)—*Chromelosporium carneum* and *C. coerulegens*—both with sexual morph unknown. For these species, the new generic name *Chromelosporiopsis* is proposed. Similar asexual morphs have also been described in some *Pachyphlodes* species of the *Pezizaceae*.

Chromelosporiopsis Hennebert, gen. nov.

MB 835622

Differs from *Chromelosporium* by its synnematus conidiophores and irregular successive bifurcate branching.

TYPE SPECIES: *Chromelosporiopsis carnea* (Schumach.) Hennebert

ETYMOLOGY: *Chromelosporium* + *-opsis*, similar to.

Ascomycota, *Pezizaceae*, sexual morph unknown.

HYPHAE septate, branched and anastomosed, fasciculating in synnemata, forming defined or effuse cushions, diversely colored (white, ochre, yellow, rose, flesh red, blue, or violet).

CONIDIOPHORES synnematos, laterally and/or apically branching in irregular successive dichotomies called here a coralloid pattern, sparsely septate, apically slightly inflated.

CONIDIOGENUS CELLS subterminal and terminal branches forming synchronously along their lengths holoblastic conidia, each on a denticle; secession rhexolytic.

CONIDIA one-celled, globose or subglobose, with thick ornamented (finely to coarsely verrucose) wall, colored in mass. seceding rhexolytically.

HABITAT: on organic soil.

***Chromelosporiopsis carnea* (Schumach.) Hennebert, comb. nov.** FIGS 12–14, 15A

MB 835623

- ≡ *Botrytis carnea* Schumach., Enum. Pl. 2: 238, 1803, nom. sanct.
- = *Isaria carnea* Pers., Ann. Bot. (Usteri) 15: 13, 1795; Syn. Meth. Fung. 2: 689, 1801.
- ≡ *Chromelosporium carneum* (Pers.) Hennebert, Persoonia 7: 196, 1973.
- = *Polyactis carnea* Ehrenb., Sylv. Mycol. Berol. 25, 1818.
- ≡ *Mucor carneus* (Ehrenb.) Link, Spec. Plant., ed. 4, 6(1): 88, 1824, nom. illeg., non Schaeff. 1774
- ≡ *Botrytis carnea* (Ehrenb.) Spreng., Syst. Veg., ed. 16, 4(1): 551, 1827, nom. illeg., non Schumach. 1803.
- ≡ *Sporodinia carnea* (Ehrenb.) Wallr., Fl. Crypt. Germ. 2: 317, 1833.
- ≡ *Ostracoderma carneum* (Ehrenb.) S. Hughes, Canad. J. Bot. 36: 792, 1958.
- = *Botrytis rosea* Link, Mag. Ges. Naturf. Freunde Berlin 7: 36, 1815, nom. illeg., non DC. 1805.
- = *Botrytis linkii* Duby, Bot. Gall, 2: 919, 1830 [as “*linckii*”].
- ≡ *Ostracoderma linkii* (Duby) S. Hughes, Canad. J. Bot. 36: 792, 1958.
- = *Campsotrichum splendidum* Schwein., Trans. Amer. Philos. Soc., n.s. 4: 283, 1832.
- ≡ *Botrytis splendida* (Schwein.) Sacc., Syll. Fung. 4: 123, 1886.
- = *Rhinotrichum opuntia* Berk. & Broome, Ann. Mag. Nat. Hist., ser. 2, 13: 462, 1854.
- = *Botrytis carnea* f. *foliicola* Roum., Fungi. Sel. Gall. Exs., Cent. 14: no. 1367, 1881.

TYPES—*Polyactis carnea* Ehrbg. [scr. Ehrenberg] on leaves of *Fagus sylvatica*, Herb. Schwaeningrichen (STR) (MBT 392408, here designated as lectotype [DAOM 83897, MUCL 2440]). *Polyactis carnea* Ehrbg. [scr. Ehrenberg] on leaves of *Fagus sylvatica*, Herb. Nees (STR) (Isolectotypes: DAOM 83896, [MUCL 2439]; Herb. Persoon (L 910-262-747) [MUCL 2464]).

Chromelosporium carneum (Pers.) Hennebert on leaves of *Quercus pedunculata* and *Fagus sylvatica*, Forest de Soignes, Tervueren, Belgium, Aug. 18 1960, leg. G.L. Hennebert (Epitype: MUCL 1208, designated as “neotype” by Hennebert, 1973; isoepitype: DAOM 74697).

COLONIES superficial, fast growing and evanescent, in scattered tufts of hyphae, 3–15 mm wide, 15–2 mm high, comprising ≤15 erect divergent synnemata

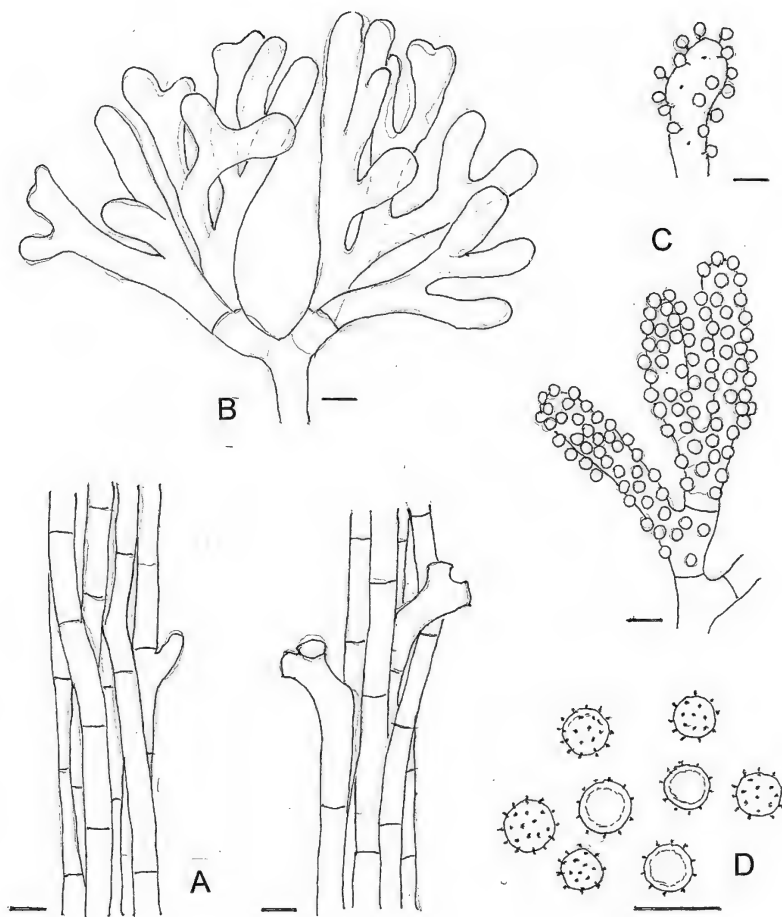


Fig. 12. *Chromelosporiopsis carnea*. A Synnemata (MUCL 1806) .B. Coralloid branching of the conidiophores. C. Conidiogenous cells. D. Verrucose conidia (B-D, isolotype MUCL 2464). Scale bar = 10 μ m.

bearing conidia in their upper half, white when young, flesh-colored when mature on the field, ochraceous salmon when dried.

HYPHAE repent, sparse, delicate, hyaline to ochraceous, single or aggregated, (9–)12–15(–23) μ m wide, thin-walled, smooth, septate, branched, often anastomosing, with short cells.

SYNNEMATA arising from the basal mat of hyphae, erect columnar, ≤ 1.5 mm high, 50 μ m wide, composed of ≤ 30 growing conidiophores.

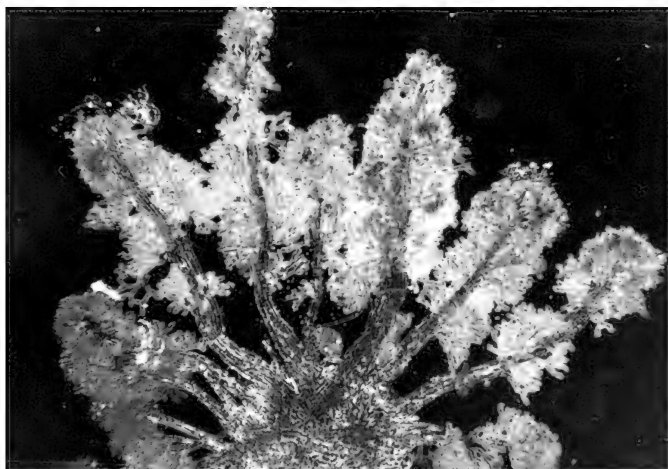


Fig. 13. *Chromelosporiopsis carnea*, cluster of synnemata with isarioid conidial head (MUCL 6278).

CONIDIOPHORES stipes contiguous, 11–17 μm wide, anastomosing, septate at 50–80- μm intervals, thin-walled, smooth, slightly bent outwards laterally and apically in the upper half of the synnemata and branching in a coralloid pattern of asymmetric dichotomies, one branch of each dichotomy developing first and sometimes becoming septate at the base,

CONIDIOGENOUS HEAD formed of 4–9 last successive bifurcations, the branches being 15–50 $\times$ 6–10 μm , apically obtuse, slightly clavate, 7–12 μm wide and often bent, all branches conidiogenous, forming an isarioid head.

CONIDIA holoblastic, borne simultaneously on denticle 1 $\times$ 0.5 μm , 5–11 μm distant from each other, one-celled, globose, occasionally subglobose, 4.8–6.6(–7.8) μm (most 5.4–6 μm), walls 1–1.5 μm thick, the inner wall ochraceous, the outer wall cyanophilic and coarsely verrucose, bearing 8–12 rounded warts in median view, seceding rhexolytically.

HABITAT: on dead leaves of *Fagus sylvatica* and *Quercus pedunculata*, also on other leaves, bark, mosses, and organic debris on soil, in forests, from August to October.

DISTRIBUTION: Europe: Austria, Belgium, France, Denmark, Germany, Great Britain, Netherlands, Sweden.

COMMENTS—The earliest description and illustration of *Chromelosporiopsis carnea* is by Persoon (1795) under the name *Isaria carnea*, with conidiophores sticking together (“conferta”), at first white, then flesh-colored (“primo albida dein carnea”) and evanescent (“evanescens”), illustrated in Persoon (1796: Observ. Mycol. 1, tab. 2 figs 6–7) by fine color paintings (FIG. 15A). The

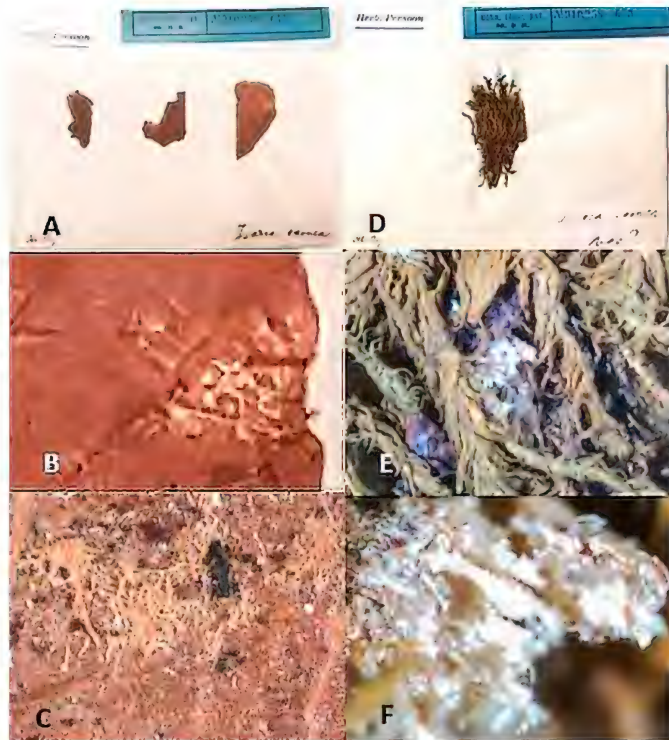


Fig. 14. Authentic specimens of *Isaria carnea* Pers. A-C. *Isaria carnea* [written by Persoon]. A. *Isaria carnea* [written by Persoon]. A. Three pieces of *Fagus* leaves. B. Enlarged immature colony. C. Enlarged collapsed synnemata. D-F. *Isaria carnea* var.? [written by Persoon]. D. Patch of moss. E-F. Enlargements of a small patch of the fungus showing young white isarioid synnemata. (Photos J. Nuytinck and Dr M. Scherrenberg, Naturalis Museum, Leiden).

authentic specimens of *Isaria carnea* in Persoon's herbarium, signed by Persoon but with no date, are here documented by the excellent photographs made by Dr Nuytinck and M. Scherrenberg in Leiden (FIG. 14). Schweinitz (1832) showed that *Isaria carnea* has fascicles of hyphae (synnemata) diverging from a shared base, pale brown, apically floccose and bearing abundant fleshy-red spores ('sporulis carneo-rubris') spread along the hyphae. *Isaria carnea* was treated by Fries (1832a,b) as a synonym of *Dactylium macrosporum* Fr., nom. sanct. [$\equiv$ *Botrytis macrospora* Ditmar, nom. illeg.], but it is really a different fungus, and its epithet is therefore potentially available for use.

However the epithet is not truly available, as Fries (1832a) accepted and sanctioned the species under the name *Botrytis carnea* based on Schumacher's description and his examination of Ehrenberg's specimens of *Polyactis carnea*.

Botrytis carnea is described as “cespitosa, stipitibus brevissimis, dichotomis, ramosissimis, albidis, sporulis congestis spicatis carneis; in lingo putrido *Betulae albae*, Septembr,” while *Polyactis carnea* shows “floccis suberectis dichotomis capitatis albis, sporidiolis primum albis, dein carneis, globosis. In foliis pinorum. Pluvio freq. In fossis. Septembr.” As neither Schumacher nor Ehrenberg cited Persoon, they are two distinct names for the same species, not obligate synonyms. As the name *Botrytis carnea* is sanctioned it must serve as the basionym for the species as understood here.

No original material of *Botrytis carnea* is available, but three good specimens collected by Ehrenberg and preserved in STR and L under the name *Polyactis carnea* contain synnemata, bifurcate branching hyphae, and verrucose conidia.

Campsotrichum splendidum Schwein. n° 2695 is described with synnemata (“coalitis floccis”), furcate branches emerging along the upper half, and bearing reddish orange verrucose conidia (“pulcherrime decorate”). This is a possible synonym of *C. carneum*.

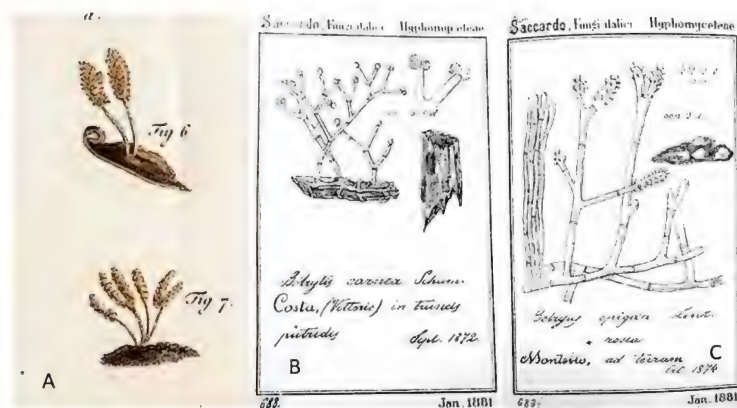


Fig. 15. A. Persoon's illustration of *Isaria carnea* in *Observ. Mycol.* 1: tab. II, fig. 6-7, 1796. B-C. Saccardo *Fungi Autografe Delineati* (1881), fig. 688: *Botrytis carnea* Schum. and fig. 689: *Botrytis epigaea* var. *rosea* Sacc.

Saccardo (1881) illustrated *Botrytis carnea* (FIG. 15B) as mononematous and dichotomous with verruculose, rose-isabella conidia without indication of synnemata. However, he drew synnemata and asymmetric bifurcations in *Botrytis epigaea* var. *rosea*, another synnematous *Chromelosporium*-like taxon (FIG. 15C). Saccardo (1886) also described *B. carnea* var. *quercina* with smaller conidia, 4.5–5 µm, asperulate and rose-colored. Both of these varieties show characters of *C. coerulescens*.

SPECIMENS EXAMINED.

AUTHENTIC SPECIMENS: **EUROPE:** (5), *Isaria carnea* [scr. Persoon] on leaves of *Fagus* leaves, Herb. Persoon (L 910-258-645). (6) *Isaria carnea* var? [scr. Persoon] on a patch of moss. Herb. Persoon (L 910-258-663) [the specimen bears immature smooth conidia]. **GERMANY:** (7) *Botrytis rosea* Link, on small pieces of leaves of *Fagus sylvatica*, Rostock. Herb. Link (B) [DAOM 51764, MUCL2451]. **UK,** (8) *Rhinotrichum decolorans* Forden, on cupules of *Fagus sylvatica*, Forden 312. Herb. M.C. Cooke 1885 (K-M) [MUCL 3495].

OTHER SPECIMENS: **EUROPE, UK** (9) *Phymatotrichum*, on bare soil and dead leaves, Ashridge, Herts., England, July 17 1955, D.A. Reid (K-M) [MUCL 2304]. (10) *Phymatotrichum* sp. on soil and vegetable debris, Windsor Great Park, Windsor, Oct. 3 1962, D.A. Reid & R. McNabb (K-M) [MUCL 3133, MUCL 3494]. (11) *Botrytis carnea*, on *Epilobium hirsutum*, Witham Park, Oxfordshire, Sept. 17 1949, M.B. & J.P.Ellis (K-M-IMI60211) [MUCL 3517]. (12) *Botrytis* aff. *splendida* Schw., on mossy *Salix* bark, Wheatfen Broad, Nrf., M.B. Ellis (K-M-IMI 26983) [MUCL 3568]. (13) *Phymatotrichum* sp. on petioles of *Petasites ovatis*, Masham, Yorks., Oct. 13 1947, S.J. Hughes (K-M-IMI 19231b) [MUCL 3572]. (14) *Phymatotrichum*, bark of *Quercus*, Kinclaven, Perthshire, Sept. 1953, M.B. Ellis (K-M-IMI63926) [MUCL 3505]. (15) *Phymatotrichum* sp., on bark and earth in a deep hole, Ashridge, Hertford. July 17 1956, D.A. Reid, det. M.B. Ellis (K-M-IMI 60584) [MUCL 3520]. (16) *Phymatotrichum* sp., on rotten wood, Ruislip Woods, Oct.14 1955, C. Booth, det. A.H.S. Brown. Herb.(K-M-IMI 61356) [MUCL 3523]. (17) *Phymatotrichum*, on moss on beach, Burnham, Beeches, Oct. 20 1956, A.H.S. Brown. (K-M-IMI 69690) [MUCL 3541]. (18) *Phymatotrichum*., oak and hazel leaf litter, Park Wood, Ruislip, Oct. 15 1949, P.K.C. Austwick (K-M-IMI 37957) [MUCL 3559]. (19) *Chromelosporium carneum*, decaying *Quercus* wood, Pett near Hastings, Sussex, Aug. 29 1965, P.C. Holland, det. W. Gams (MUCL 7929). (20) *Chromelosporium carneum*, on stem debris, Ashdown Forest, Forest Row, Sussex, Oct. 1 1967, D. Mitchell & P.C. Holland (MUCL 11290). **NETHERLANDS** (21) *Botrytis fulva* Link ex Fr. on herbaceous stems under *Fagus sylvatica*. Bussum, Oct. 24 1929, W.J. Lütjeharms (L) [DAOM 83937, MUCL 2515]. **AUSTRIA** (22) *Botrytis carnea* Schum. ad folia et cortices putridis, sylvis umbrosis, autumnu, L. Fuckel. Fuckel Fungi. Rhen. Exs. 146 (G, K-M, GRO, NY) [DAOM 74694, MUCL 1808]. **DENMARK** (23) *Phymatotrichum*, on leaves, wood and cupules of *Fagus sylvatica*, Gris Skov, Sealand, Oct. 2 1955, S.J. Hughes (DAOM 51702). (24) *Phymatotrichum*, on wood chips of *Fagus sylvatica*, Gris Skov, Sealand, Oct. 2 1955, S.J. Hughes (DAOM 51690). **POLAND:**(25) *Botrytis carnea* Schum., in trunco *Juniperi*, Eichler, in herb. Bresadola 184 (S) [DAOM 83948, MUCL 2532]. (26) *Chromelosporium carneum*, on rotten wood, Biatowiesga forest, Pologne, Sept.5 1966, W. Gams (MUCL 9298). (27) *Chromelosporium carneum*, on rotten wood, Augustow Reserve, Starozym, Pologne, Sept.3 1966, W. Gams (MUCL 9299). **FRANCE** (28) *Botrytis fulva* Link écorce de *Quercus* et *Corylus*, Lyon, Sept. 1879, J. Therry. C. Roumeguère Fungi Gall. Exs. (BR) [DAOM74695, MUCL 1809]. (29) *Botrytis carnea*. feuilles de chêne [*Quercus*] pourrissantes, Tassin, Lyon. Sept. 1880, Cryptogames du Lyonnais, J.J. Therry. 5092 (PAD) [MUCL 1870]. (30) *Phymatotrichum*, on mossy bark of *Quercus*, Forêt de Jupilles, France, Sept.15 1952, E.M. Wakefield, det. M.B. Ellis (K-M-IMI 50643) [MUCL 3598]. **BELGIUM** (31) *Botrytis rosea* Link, in foliis

Quercus robur, coll. Libert (BR) [DAOM 74693, MUCL 1806]. (32) *Chromelosporium carneum*, on dead leaves of *Fagus sylvatica* and *Quercus pedunculata* in woods, Parc d'Arenberg, Hevelee, Sept. 1 1960, G.L. Hennebert (MUCL 1218, DAOM 74698). (33) *Chromelosporium carneum*, on twig of *Fagus sylvatica*, Parc d'Arenberg, Hevelee, Août 21 1964, G.L. Hennebert (MUCL 6278). (34) *Chromelosporium carneum*, on bare humid soil under *Fagus sylvatica*, in Lauzelle forest, Louvain-la-Neuve, Oct. 2017, G.L. Hennebert (MUCL 56651).

***Chromelosporiopsis coeruleascens* (Bonord.) Hennebert, comb. nov.** Figs 16–18

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- ≡ *Polyactis coeruleascens* Bonord., in Fresenius, Beitr. Mykol. 1: 14, 1850.
- ≡ *Botrytis coeruleascens* (Bonord.) Sacc., Syll. Fung. 4: 132, 1886.
- ≡ *Chromelosporium coeruleascens* (Bonord.) Hennebert, Persoonia 7:197, 1873.
- = *Hyphelia purpureospadicea* Fuckel, Jahrb. Nassauischen. Vereins Naturk. 23–24: 363, 1870.
- ≡ *Botrytis purpureospadicea* (Fuckel) Sacc., Syll. Fung. 4: 121, 1886.
- = *Botrytis epigaea* subsp. *rosea* Sacc., Michelia 2(8): 544, 1882.
- ≡ *Botrytis epigaea* var. *rosea* (Sacc.) Sacc., Syll. Fung. 4: 136, 1886.
- = *Botrytis carnea* var. *quercina* Sacc. Syll. Fung. 4: 119, 1886.

TYPES: *C.[Chromelosporium] rhodianthinum* n.sp. -[prov.name] on rotting leaves and humic debris of *Acer saccharum*, *Betula lutea* and *Tsuga canadensis* in mixed woods, Bell's Corners, Ontario, Canada, 18.07.1961, leg. G.L. Hennebert (Neotype: DAOM 83371, designated in Hennebert 1973; Isonotype: MUCL 2323).

COLONIES in tufts, appearing and rapidly evanescent, with ≤20 synnemata arising from a basal mat of hyphae, at first white to bluish, sky-blue turning to rose-lilac, finally vinaceous ocher at maturity in fresh conditions and vinaceous brown when dried.

HYPHAE superficial, sparse, delicate, hyaline, thin-walled, smooth, forming mats 1–5 mm wide, 1 mm high, hyphae interwoven 11–29 µm wide, septate into 32–46 µm long cells.

SYNNEMATA erect, divergent, composed of ≤25 hyphae, septate and anastomosing, the central hyphae growing first ≤800 µm high, the outermost ones shorter, each hyphae serving as a conidiophore stipe.

CONIDIOPHORES stipes hyaline, 6–9 µm wide, septate, with 36–54 µm long cells, thin-walled, smooth, all branching at the top, in successive, asymmetric dichotomies in a coralloid pattern, forming a globose or somewhat conical conidial head.

CONIDIOGENOUS HEAD comprising all branches of the conidiophore except the first ones, 15–75 (mostly 30–60 µm) µm long, 9–12 µm wide, the distal cells clavate ≤15 µm wide, obtuse, forming conidia almost simultaneously.

CONIDIA holoblastic, on denticle 1 × 0.5 µm, 4–9 µm spaced, one celled, globose, 4.2–6.6 µm, most 5.4 µm, walls 1 µm thick, subhyaline, the outer

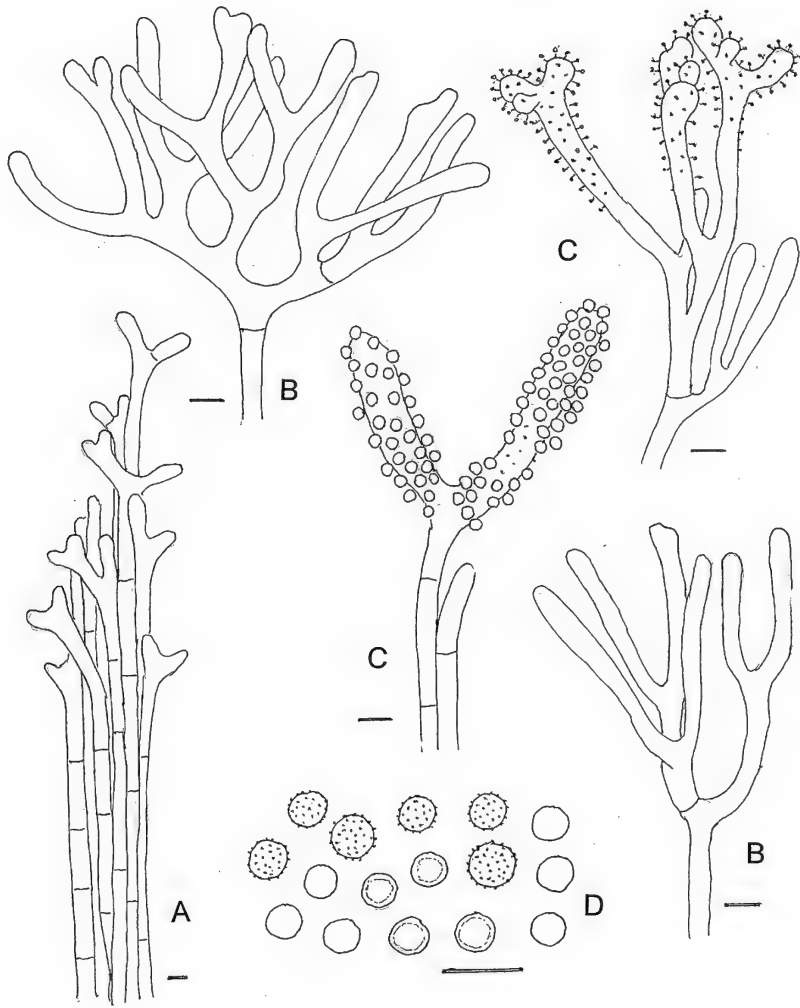


Fig. 16. *Chromelosporiopsis coerulescens* (neotype DAOM 83371).
A. Synnemata B. Asymmetric dichotomies or coralloid branching. C. Conidiation.
D. Finely verrucose conidia. Scale bar = 10 μ m.

wall finely punctate ('minutissime asperulis', Saccardo 1886 p. 132), with 12–18 small warts in median view, seceding rhexolytically.

HABITAT: on mosses, rotten wood debris, tree leaves, conifer needles in humid forest.

DISTRIBUTION: North America: Canada, USA, Europe: France, Belgium.

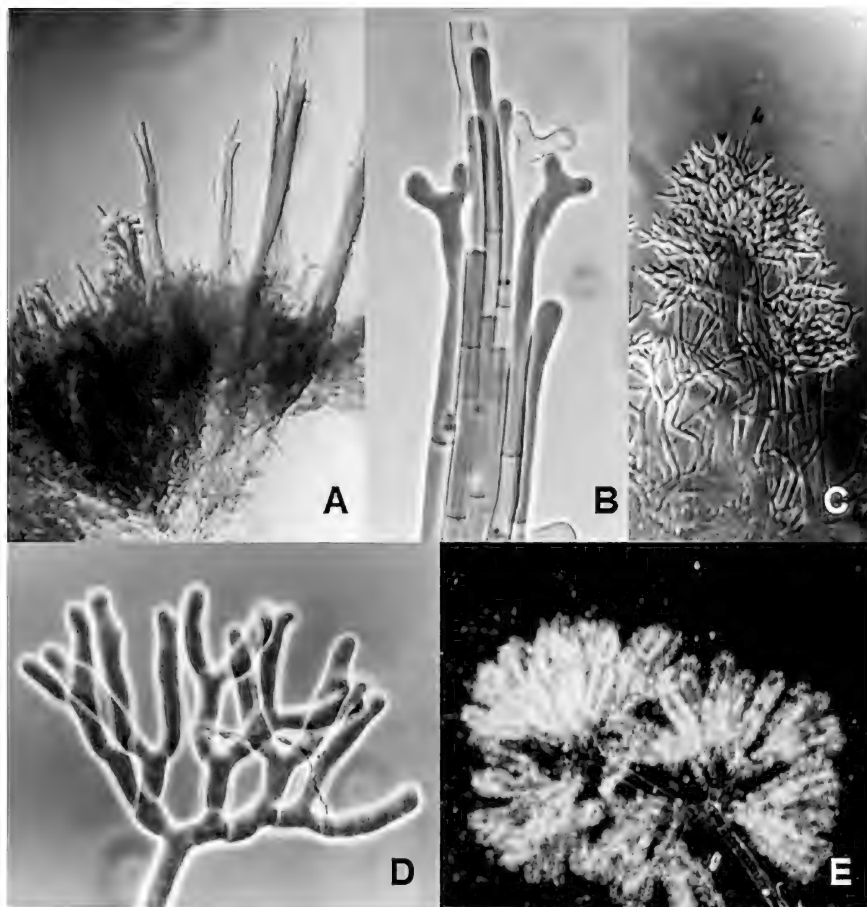


Fig. 17. *Chromelosporiopsis coerulescens* (neotype DAOM 83371). A. Fungus mat with emerging young synnemata. B. Top of growing synnema. C. Head of branches. D. Asymmetric dichotomous branching. E. Conidial head.

COMMENTS—Fresenius (1852: 74), who received a specimen and a description of the species from Bonorden, noticed that “die sporen sind rund, feinwarzig, nicht glatt wie Bonorden angibt”. Indeed Bonorden (1851) described the spores as “glatt”. Fresenius also illustrated the conidiogenesis of the species.

Chromelosporiopsis coerulescens differs mainly from *C. carnea* by the colour when young, the synnematal development, the narrower conidiophore hyphae, and the smaller, punctate conidia.

Bonorden (1851) described *Polyactis coerulescens* as “zuerst weisse, dann hellblau, zuletzt durch die Sporen bräunlich.” The pale blue (hellblau) young

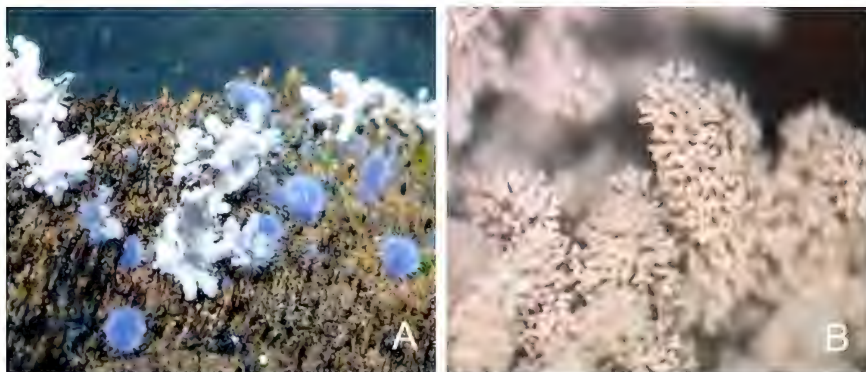


Fig. 18. *Chromelosporiopsis coerulescens*. A. Young blue cushions and white young synnemata. B. Rose-lilac nearly mature synnemata (specimens collected and photographed on rotting trunk on the ground, A. 14.06.2014, Sainte-Cécile-de-Masham, QC and B. 19.08.2018, Orleans, Ont, Canada, by Jonathan Mack, Mycoquebec.org).

stage of the colonies changes during maturation to rose-lilac-mauve and then vinaceous ochre-brown.

Fuckel (1870) described under *Hyphelia* the new species *H. purpureospadicea*. It is here a synonym of *C. coerulescens* after examination of the holotype.

Labbé (2015) describes the species as “remarquable par ses colorations bleu cristal puis rose-violet et ressemblant presque à des cristaux en forme d’aiguilles.” The species is illustrated in its change of colour in the photographs by Jonathan Mack (Fig. 16) in J. Landry on mycoquebec.org and in photographs by Cornell Mycology (Hodge 2017).

SPECIMENS EXAMINED

TYPE & AUTHENTIC SPECIMENS EUROPE: GERMANY (2) *Hyphelia purpureospadicea* Fuckel, ad terram arenosam humidam in sylvis acerosis, raro, Autumno, circa Budenheim, Fuckel. Fungi Rhen. Exs. 2214 (G, holotype; BR, GRO, PAV, FH, isotypes) [DAOM 83395, MUCL 2396].

OTHER SPECIMENS. NORTH AMERICA: CANADA (3) *Botrytis* ?, on humus, Morgan’s woods, MacDonald College, near Montreal, Qué., Aug. 27 1941, R.F. Cain 12979 (DAOM 80136) [MUCL 2276]. **USA (4)** *Botrytis dichotoma*, on ground and rotting wood, Fall Creek, Ithaca, N.Y., June 18 1894, G.F. Atkinson. Herb. Atkinson 1153 (CUP) [DAOM 84693, MUCL 2876]. **(5)** *Botrytis terrestris*, on humic ground under conifers, Shelburne, New Hampshire, Sept. 1891, W.G. Farlow (FH) [DAOM 84699, MUCL 2883]. **(6)** *Botrytis terrestris*, on dead leaves, trunks, dungs, etc. in conifer woods, Shelburne, W.G. Farlow (FH) [DAOM 84700, MUCL 2884]. **(7)** *Botrytis epigaea*, on rotten wood and mosses, Hadley Lake, Machias, Sept. 21 1898, W.G.

Farlow 36 (FH) [DAOM 84698, MUCL 2882]. (8) *Botrytis epigaea* Link, on mosses, Magnolia, Mass. July, W.G. Farlow (FH, UPS, CUP) [DAOM 84912, MUCL2484]. (9) *Botrytis epigaea*, on *Hydnum*, Gerrish Island, Kittery Pt., Maine, R. Thaxter (FH) [MUCL 2892]. (10) *Botrytis (Polyactis) coerulescens* (Bon.) Sacc., on bare soil in forest, Lingle Valley, Mifflin Co., Pa., July 3 1938, L.O. Overholts 21176, D.H. Linder (FH) [MUCL 2891]. (11) *Hyphelia terrestris*, on decaying leaves, Ringwoods, N.Y., Sept. 6 1952, R.F. Cain (TRT 24143) [MUCL 2863]. (12) *Ostracoderma*, on *Quercus* rotten wood, Pennsylvania state, July 4 1957, E.A. Atwell n° 5779 (DAOM 59233). (14) *Ostracoderma*, on lawn, College Park, Maryland, Sept. 15 1961, A.M. Golden, C.R. Benjamin (BPI) [MUCL 2957].

EUROPE: BELGIUM (15) *Hyphomycete* n° 517, sur sol de jardin, Rue Berchmans, Bruxelles, June 21 1917, M. P. C. Beeli (BR). (16) *Botrytis violacea/lilacina* Schw, sur argile, Forêt de Soignes, Sept. 23 1933, Bommer (BR).

Species of *Pezizaceae* with known sexual morphs and similar synnematous conidiophores and conidiogenesis

A similar *Chromelosporiopsis* asexual morphology was found in specimens collected by Korf (1994) and identified by Healy & al. (2015) as *Pachyphlodes pfisteri* Tocci & al. (*Pezizaceae*), and briefly described by Hennebert (2017).

In October 2017, some samples of synnematous *Chromelosporiopsis* conidial mats were collected on bare soil in forests around Louvain-la-Neuve in Belgium. The DNA sequencing in MUCL identified three samples as *Pachyphlodes nemoralis* Hobart & al., and one sample as *P. citrina* (Berk. & Broome) Doweld. Their conidial morphs are clearly distinguished by the synnematal structure and hyphal width, the hyphal length and width of the conidiophore coralloid branches, and particularly by the conidial size and the conidial wall ornamentation (Hennebert & Decock 2020).

Pachyphlodes nemoralis has globose conidia, 4–6.5 µm wide, with 0.5 µm thick walls covered with ≤0.3 µm high tuberculate warts (12–14 in median view).

Pachyphlodes citrina has globose conidia, 4.5–7 µm wide, with 0.5 µm thick walls covered with ≤0.8 µm high baculate warts (12–14 in median view).

3. Doubtful and excluded taxa

Most synnematous *Chromemosporium*-like herbarium specimens examined were labeled as *Botrytis epigaea*, *Polyactis epigaea*, *Hyphelia terrestris*, or *Phymatotrichum*, among others. These names are considered below.

Botrytis epigaea Link, Spec. Plant., ed. 4, 6(1): 52, 1824.

≡ *Polyactis epigaea* (Link) Bonord., Handb. Mykol.: 115, 1851.

≡ *Phymatotrichum epigaeum* (Link) Vasyag., in Shvartsman & al., Flora Sporov. Rast. Kazakhst. 8: 263, 1973.

No authentic material of *Botrytis epigaea* or *Polyactis epigaea* was retrieved from relevant herbaria. Link (1824) originally described *Botrytis epigaea* as: “*Botrytis epigaea*, thallo effuso, floccis sporodiferis subramosis brevibus, sporidiis globosis minutis. Habitat in terra humida sylvarum Germaniae. Lecta Berolini im Thiergarten (Lk.) (v.v.)” This nine-word description being applicable to a number of fungi, the name is doubtful in absence of authentic specimen. Fries (1832a,b) did not accept the species in *Sporotrichum* because he considered it as only mycelium.

Bonorden (1851) interpreted Link’s species under *Polyactis epigaea* in his Fig. 161 as a fungus showing bifurcate conidiophores covered with conidia, adding that the colour of the mature mass of spores is gray or greyish yellow (“grauen oder graugelben Pulver”). This might suggest a *Chromelosporium*-like species, but no authentic material is extant.

The earliest specimen received as *Botrytis epigaea* was collected by Fuckel in 1861. This synnematus *Chromelosporium*-like fungus with punctate conidia does not possess enough for identification.

Saccardo (1886) considered *Botrytis epigaea* similar to *Hyphelia terrestris* sensu auct.

Phymatotrichum Bonord., Handb. Mykol.: 116 (1851).

Bonorden, who defined his genus with conidiophores branched tree or shrub-like, not umbellate, bearing on their distal swollen branches pedicellate conidia (“gestielte Sporen”), described three species: *P. gemellum*, *P. pyramidale*, and *P. laneum* (FIG. 19).

While *P. pyramidale* Bonord. was transferred to *Botryosporium*, Saccardo interpreted *P. laneum* as *Botrytis laneus* (Bonord.) Sacc. and *P. gemellum* as *B. gemella* (Bonord.) Sacc.; Hennebert (1973), who interpreted *P. gemellum* as *Botrytis cinerea* Pers., deduced that *Phymatotrichum* was a synonym of *Botrytis*.

But none of the researchers considered the pedicellate conidia (“gestielte Sporen”) mentioned by Bonorden as a diagnostic generic criterion, which is neither a character of *Botrytis* nor of *Phymatotrichopsis* (FIG. 20). *Phymatotrichum gemellum* is described with some fasciculate superficial hyphae (“verbundenen hypha”) bearing short tufts ending in unequal

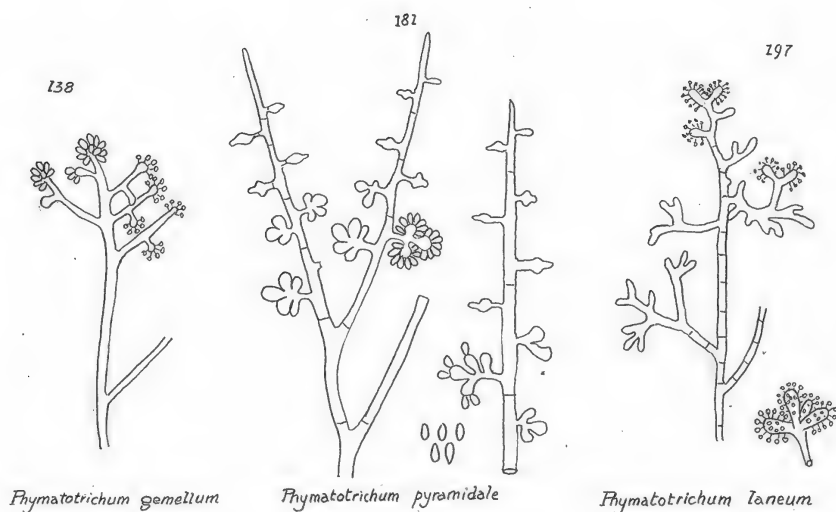


Fig. 19. Copy of the Bonorden's illustrations of the species of *Phymatotrichum*.

bifurcate apical swollen fertile cells (“Endäste erweitern sich zu zwei ungleich grossen Basidien”), characters that possibly suggest species of *Chromelosporiopsis*. But Bonorden commented that the species possessed characters of both *Polyactis* and *Botrytis*, but absent any authentic material, the genus remains doubtful.

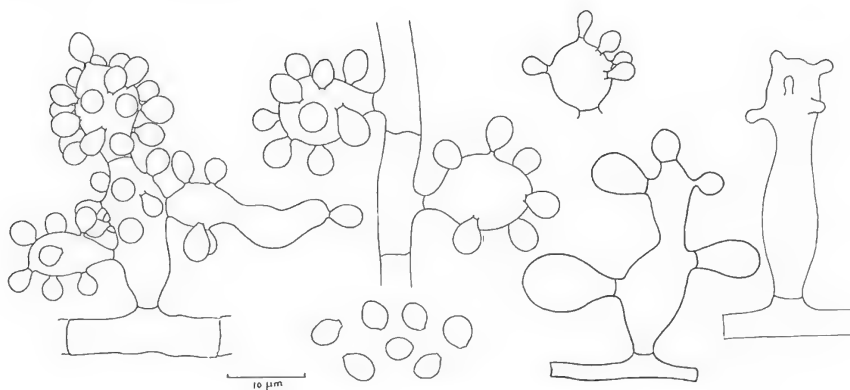


Fig. 20. Conidiogenesis of *Phymatotrichopsis omnivora* (Shear) Hennebert from dried sporemat on soil in cotton field, Paris, Texas, Sept. 18, 1915, BMD, received from Missouri Bot. Garden June 1916 (FH) [MUCL 2868] (Marek et al. 2009).

Phymatotrichum silvicola Taubenh. & G.M. Watkins,
Amer. J. Bot. 24: 390, 1937 [as "*silvicolum*"].

SPECIMENS EXAMINED: (1) *Phymatotrichum silvicolum* Taubenh. and Watkins, on post oak wood on sandy soil near Bryan, Brazos Co, Texas, November 1936 (NY) [DAOM 84656, MUCL 2690]. (2) *Phymatotrichum silvicolum* Taubenh. and Watkins, on post oak wood on sandy soil near Bryan, Brazos Co, Texas, Sept.8, 1937 (BPI) [DAOM 84657, MUCL 2691].

Two authentic specimens of *Phymatotrichum silvicola* were received. The fungus is described from Texas on sandy soil in forest, as "hyphal mats more or less circular, 0.5–4 cm wide, white becoming greyish yellow, with synnemata of conidiophores arising from them, with bifurcate branching, the apical branches clavate, 5–8 μ m wide and covered with subglobose one-celled conidia 2–4.6 μ m wide on denticles". The specimens are ambiguous, containing globose (3.5–5.2 μ m) punctate conidia mixed with napiform to globose (6.5–8.7 μ m) verrucose conidia.

Rhinotrichum thwaitesii Berk. & Broome, Ann. Mag. Nat. Hist., ser. 2, 7: 177, 1851.

SPECIMEN: *Rhinotrichum thwaitesii* Berk. & Broome, Clifton, Berkeley. Herb. Berk. (K-M), holotype, with included watercolour plate by Berkeley [MUCL 2952].

The specimen contains conidiophores branched in dichotomies bearing globose conidia on denticles with very verrucose walls, but no synnemata have been seen. *Rhinotrichum thwaitesii* remains a doubtful species in view of the discrepancies between the fungus and Berkeley's accompanying watercolour plate and the published diagnosis of the name with ovoid and larger spores.

Isaria thyrsoides Penz. & Sacc., Malpighia 15: 251, 1902.

Isaria thyrsoides, found on rotting leaves, insects and dung, in Tjibodas, Java, 1897, is described as white tufts of erect cylindrical synnemata 1.5 mm high, 40–50 μ m wide, made of septate hyphae that emerge laterally and apically from the upper half of the synnemata as bi- and tri-furcated conidiogenous branches, 5.5–6 μ m wide, sparsely septate and covered on denticle ("subsessile") with smooth globose conidia 3.5–4 μ m wide (FIG. 21). The fungus is turns ash-grey at maturity. Are the conidia really smooth? Despite the colour of the

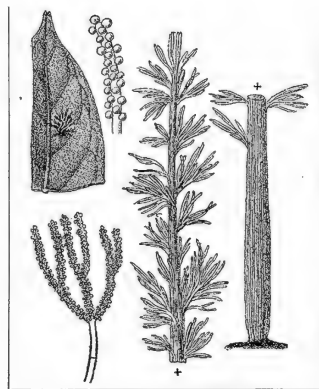


Fig. 21. *Isaria thyrsoides* Penzig & Sacc., Malpighia 15: 251, 1902

fungus and the smooth conidia, the description suggests a *Chromelosporiopsis* species. The original material needs to be located and re-studied.

Chromelosporium terrestre (Fr.) M.B. Ellis, More Demat. Hyphom.: 154, 1976.

≡ *Hyphelia terrestris* Fr., Syst. Mycol. 3(1): 213, 1829, nom. sanct.

Ellis (1976) proposed the combination *Chromelosporium terrestre* for the basionym *H. terrestris* in order to correct the then illegitimate name *Chromelosporium tuberculatum* (Hennebert 1973). But *Hyphelia terrestris* is not a *Chromelosporium*-like species as shown below. The fungus described and illustrated by Ellis under that name is an unidentified species of *Chromelosporiopsis* and belongs to the set of collections considered hereunder.

Unidentified herbarium material with features of *Chromelosporiopsis*

Beside the presence of synnemata, a generic character, the specific microscopic characters of *Chromelosporiopsis* (observed when possible in the following material) are the hyphal widths (diameters), the branching patterns, the conidial size, and the ornamentation of the conidial wall. The conidial wall ornamentation serves as an important criterion distinguishing between asexual morphs of *Pachyphlodes* species (Hennebert & Decock 2020) and is used here as a basis for a preliminary grouping of the specimens. But a good characterization of the wall ornamentation requires high quality equipment without which the present groups are based only on the number of warts visible on median view of the conidia and not on the wall morphologies. The specimens are classified according to the conidial wall surfaces ranging from punctate to coarsely warty. To be diagnostic, the number of median warts must be combined with wart morphology.

SPECIMENS EXAMINED

CONIDIA PUNCTATE (≥18 WARTS, MEDIAN VIEW)

AUTHENTIC SPECIMEN EUROPE: (3) *Trichoderma laeve* ? Pers., frequens in sylvulis prope Parisios [scr. Pers.] Herb. Pers. (L 910.267.31) The fungus is immature and fragmentary. [DAOM 83899, MUCL 2461].

OTHER SPECIMENS. EUROPE: GERMANY (4) *Botrytis epigaea* Link, *Polyactis epigaea* Bon., Giesen, Oct. 22.1861, Herb. Fuckel in herb. Barbey-Boissier (G 005439) MUCL 2400)]. (5) *Botrytis epigaea* Link, ad terram Bavaria, Killermann. Herb. Bresadola (BPI) [DAOM 83891, MUCL 2428]. SWEDEN (6) *Hyphelia terrestris*, ad terram nudam, Stollsbaden, Uppsala, Aug. 7 1932, Seth Lundell. Flora Suecica (UPS) [DAOM 83921, MUCL 2494]. (7) *Hyphelia terrestris*, at the lower course of the rivulet Skytebäcken, Hälsungland, Färila parish, Skyte, Aug. 2 1956, J.A. Nannfeldt. Flora Suecica 14770 (UPS) [DAOM83905, MUCL 2770]. (8) *Hyphelia terrestris*, Zögenern Wald, b. Lündensitz, Aug. 1844 (PR 181907) [DAOM 84707, MUCL 2907]. UK (9)

Ostracoderma, on wet soil, Wotten under Edge, Gloucestershire, Aug. 1961, R.W.G. Dennis (K-M-IMI 89255) [DAOM 83951, MUCL 2541]. (10) *Botrytis splendida* Schw., on soil, Skircoat Green, Halifax, Yorkshire, Nov. 1955, R. Watling, det. M.B. Ellis (K(-M-IMI 61440) [MUCL 3524]. FINLAND (11) *Hyphelia terrestris* = *Botrytis epigaea* Link var. *rosea* Sacc. on soil, Mustiala, Aug. 25 1869, P.A. Karsten, W. Nylanders, Herb. P.A. Karsten (H) [DAOM 83903, MUCL 2470]. (12) *Hyphelia terrestris*, supra terram, Mustiala, Aug. 1865, P.A. Karsten. Flora Fennica (UPS) [DAOM 83913, MUCL 2485]. NETHERLANDS (13) *Ostracoderma* (? *Tomentella granulata* Bref.), op naakte bodem in loofbos lenig humensegrond, Ulvenhout, Ulvenhoutse bos, Sept. 29 1959, R.A. Maas Geesteranus 13006 (L) [DAOM 83935, MUCL 2513]. PORTUGAL (14) *Botrytis carnea* Schum., ad terram, Portugal, Torrend 21, Herb. Bresadola (S) [DAOM 83946, MUCL 2528]. BELGIUM (15) *Hyphelia*, on bare soil, Forêt de Soignes, Tervueren, Aug. 16 1960, G.L. Hennebert (MUCL 1214) [DAOM 83904]. DENMARK (16) *Ostracoderma*, ad terram in sylva faginea, Sjaelland, Sonnerup sogn., Ovdруп skov, Sept. 13 1952, Mykologisk Kongres, J.A. Nannfeldt. Flora Danica 12552 (UPS) [DAOM 83915, MUCL 2488].

NORTH AMERICA: CANADA (17) *Ostracoderma*, on garden soil, in gras, Ottawa, Oct. 15 1960, V.J. (MUCL 1534). (18) *Botrytis epigaea*, on soil in barley field, Glen Williams, Halton Co., Ont., Sept. 9 1956, R.F. Cain (TRT 32547) [DAOM 84686, MUCL 2860]. USA (19) *Rhinotrichum thwaitesii* B. & Br., on ground in woods, south side of Fall Creek, Ithaca, June 25 1959, G.F. Atkinson, Herb Atkinson 22860 (CUP) [DAOM 84695, MUCL 2878]. (20) *Hyphelia terrestris* on ground, Nashville, York Co., Ont. Sept. 29 1956, R.F. Cain (TRT 32443) [DAOM 84685, MUCL 2859]. USA (21) *Botrytis isabellina* Pr., on bark of *Pinus sylvestris*, Jumby Lawn, Boston, Nov. 1906, H.C. Hawley (BM) [MUCL 2280]. (22) *Hyphelia terrestris*, on damp ground in woods, Bois Mallet, West La. May 23 1886, A.B. Langlois 412 (BPI) [DAOM 83892, MUCL 2429]. (23) *Hyphelia terrestris*, on sandy soil in field, Nashville, York. Co. Ont. Oct. 9 1955, R.F. Cain, Herb. RFC 31601 (WU) [MUCL 2408]. (24) *Botrytis epigaea* Link, on moist humus and soil, Altamonte, Florida, Aug. 1 1957, P.O. Schalbert, P.L. Lentz (BPI) [MUCL 2960].

AUSTRALASIA: AUSTRALIA (25) *Phymatotrichum*, on dead leaves, twigs and woody fruits, Brisbane, Australia, June 1951, R.F. Langdon 817 (K-M-IMI 54841) [MUCL 3504]. NEW ZEALAND (26) *Botrytis terrestris*, snow white patch on soil, New Zealand, W. Odenso. Herb. J.B. Ellis (NY) [DAOM 84680, MUCL 2851].

CONIDIA VERRUCOSE (12-16 WARTS, MEDIAN VIEW)

EUROPE: AUSTRIA (1) *Hyphelia terrestris* var. *flava*, ad terram humidam in dumestis, non raro, Autumnno, Oestrich, Fuckel. Fuckel Fungi Rhen. Exs. Supp. 1641 (Symb. Mycol.: 363 1869) (G, GRO, BM, FH) [DAOM 83327, MUCL 2258]. ITALY: (2) *Botrytis epigaea* Link. Padova, ad terram udam umbrosam, December. 1874. Saccardo P.A. Mycotheca veneta [Cent. IV, 1876] 360. [MUCL 2283] (3) *Botrytis epigaea* Link, a) ad terram nudam in Horto Botanica Ticinensi, b) ad terram herbosam sub cupuliferis, ibidem. Ipse lege. Autumnno. Forma b *rubella* ad var. *roseam* Sacc. ferendo mihi videtur, quamvis conidia paulum majora sint. Cavara F. Fungi Longobard. Exs. 145 (B, K-M, S, L 910.224-184) [DAOM 83335, MUCL 1805 = 2285]. (3) (4) *Botrytis epigaea* Link, ad terram, Florentiae, June 1891, N. Martely, Herb. Bresadola (S) [DAOM 83939, MUCL 2516]. GERMANY (5) *Hyphelia terrestris* ad vias nemorum, Grossen Garten, prope Dresden. Rabenh. Klotzschii Herb. Viv.

Mycol. I, 1846 (PR, PAV, BR) [DAOM 83895, MUCL 2432]. (6) *Hyphelia terrestris*, in parnecio Tyrois, Aug. 29 1859, P.A. Karsten (H) [DAOM 83902, MUCL 2469]. **SWEDEN** (7) *Hyphelia pulvinata* (Fr.) Juel, på sandjord utmed en väg I baarskog, Uppland, Uppsala, Stadsparken nära Norby, Oct. 1933, Seth Lundell. Flora Suecica 1068 (UPS) [DAOM 83910, MUCL 2482]. (8) *Hyphelia pulvinata* (Fr.) Juel, på naken jord I vågkant, Uppland, Estuna, Ljushammaren, Malmö, Sept. 27 1955, Seth Lundell. Fungi Suecici (UP) [DAOM 83917, MUCL 2490]. (9) *sine nomine*, auf nackter Erde, in Park, Uppland, par. Solna, Aug. 1906, L. Romell, Herb. Mykol. Lars. Romell 17715 (S) [DAOM 83944, MUCL 2523]. (10) *Polyactis epigaea* (Link) Bon, ?*Hyphelia*, auf nackter Erde auf einen Pfaden Upl. Stockholm: Ekbacken, Jul. 22 1894, L. Romell. Herb. L. Romell (S) [DAOM 83945, MUCL 2526]. **NETHERLANDS** (11) *Ostracoderma*, op de gronde in loofbos, Ulvenhout, Ulvenhouter bos, Oct. 6 1959, R.A. Maasgesteranus 13025 (L) [DAOM 83936, MUCL 2514]. **FRANCE**: (12) *Hyphelia terrestris*, in umbrosis viis, Montmorency, St Germain, Fontainebleau Sept. 1842-1848, Roussel, Herb. E Roussel (PC) [DAOM 84661, MUCL 2703]. **BELGIUM** (13) *Chromelosporium*, sur le sol d'un chemin en forêt, Bois de Hevelee, Heverlee, Brab., G.L. Hennebert (MUCL 6701). (14) *Hyphelia?*, sur soil humide, au bord d'un chemin ombragé, Forêt de Soignes, Groenendael, Aug. 16 1960, G.L.H. (MUCL 1205, DAOM 74900).

NORTH AMERICA: CANADA: ONTARIO (15) *Ostracoderma*, Bells Corners, Ont. Sept. 10 1961, G.L. Hennebert (DAOM 83922, MUCL 2496). **USA: VIRGINIA** (16) *Botrytis epigaea* Lk. var. *rosea* Sacc., on dead leaves, Limberlost, Shenandoah National Park, Va., Sept. 9 1937, J.A. Stevenson and V.K. Charles (BPI) [MUCL 2409]. (17) *Botrytis epigaea* Link, on soil under leaves, Arlington cementary, Virginia, May 22 1932, C.L. Shear (BPI) [DAOM 83870, MUCL 2427]. **CONNECTICUT** (18) *Botrytis fulva* Link, near *B. epigaea*, on soil and grass, New Haven, Conn. July 6 1889, R. Thaxter, Herb. Atkinson (CUP) [DAOM 84696, MUCL 2879]. **MASSACHUSETTS** (19) *Botrytis spectabilis*, on rotten wood, Prospect Hill, Waltham, Oct. 1901, W.G. Farlow (FH) [DAOM 84701, MUCL 2885]. (20) *Botrytis epigaea*, near *Hyphelia terrestris*, on rotten wood in humic litter, Bedford, Mass., Sept. 1901, W.G. Farlow (FH) [DAOM 84697, MUCL 2881]. **NEW MEXICO** (21) *Rhinotrichum roseum*, on buried dead leaves, Chirlehunt, Sept. 1854. Herb. Currey (K-M) [MUCL 2300].

CONIDIA VERY VERRUCOSE (6–12 WARTS, MEDIAN VIEW)

EUROPE: SWEDEN (2) *Hyphelia terrestris*, on soil, Kronoparken, Uppsala, Uppland, Aug. 1916, H.O. Juel. Flora Suecica (UPS) [DAOM 83911, MUCL 2483]. (3) *Hyphelia pulvinata* (Fr.) Juel, på naken jord I strandsnåret, Upland, Naturpark Bondkyrka, Värdsåtra, Jul. 18 1930, Set Lundell. Flora Suecica 0798 (UPS) [DAOM 83909, MUCL 2481]. (4) *Hyphelia*, ad terram nudam sub *Corylus*, öland, Persmäs parish, Legenäs, Aug. 3 1953, J.A. Nannfeldt. Flora Suecica 13327 (UPS) [DAOM 83906, MUCL 2477]. **DENMARK** (5) *Ostracoderma*, ad terram in fageto, Sjealland, Hvaloo skov, Sept. 14 1952, Mykologisk Kongress, J.A. Nannfeldt. Flora Danica 12603 (UPS) [DAOM 83919, MUCL 2492]. **UK** (6) *Ostracoderma pulvinatum* Fr. Sibbertoft, 1873, Berkeley, Herb. Berk (K-M) (conidia with prominent blunt warts, drawn by Berk.) [MUCL 3497]. (7) *Phymatotrichum*, on burn ground and wood, Ashridge, Herts., England, Oct. 9 1955, D.A. Reid (K-M) [MUCL 2303]. **GERMANY** (8) *Botrytis epigaea* Link., ad terram humidam, non frequens. Aestate. circa Schlangenbad. L. Fuckel. Fuckel Fungi Rhen. Exs. 2301, 1871 (G, K-M, B, K, GRO) [MUCL 2282].

FRANCE (9) *Hyphelia terrestris*, ad vias in sylvis Fontainebleau, Aug. 4 1869, Roussel, Herb. E. Russel (PC) [DAOM 84662, MUCL 2704]. **BELGIUM** (10) *Chromelosporium*, sur le sol en forêt, Bois de Bonsecours, Blaton, Hainaut, G.L. Hennebert (MUCL 6332).

CONIDIA SMALL, COARSELY VERRUCOSE (4–6 WARTS, MEDIAN VIEW)

EUROPE. SWEDEN (1) *Hyphelia*, on bare soil under stormfelled spruce, Gastrikland, Hills in Tolfforskogen, near Tolffors, Aug. 15 1954, J.A. Nannfeldt. Flora Suecica 11065a (UPS) [DAOM 83908, MUCL 2480].

NORTH AMERICA: CANADA: QUÉBEC (2) *Botrytis?*, on humus, Morgan's woods, MacDonald College, near Montreal, Qué. Aug. 27 1941, R.F. Cain 12979 (DAOM 80136) [MUCL 2276]. **USA: NEW YORK** (3) *Phymatotrichum*, on soil, Lloyd Cornell Preserve, Slatterville, NY, Sept. 6 1952, W.W. Diehl (BPI) [DAOM 83889, MUCL 2426].

Re-evaluation of *Hyphelia terrestris*

Identification of the majority of the examined herbarium specimens found to be synnematus *Chromelosporium*-like species as *Hyphelia terrestris* is based only on the short macroscopical description and habitat information by Fries (1829): “effuse, strigoso-tomentosa, candida, medio evanescens, sporidiis subargillaceis ... in terra humosa, umbrosa, humida and denudata” and ignores Fries's synonymy.

The signed and dated specimens among the specimens examined show that this interpretation was accepted as early as in 1842 by Roussel, 1846 by Rabenhorst, 1861 by Fuckel, 1865 by Karsten, 1886 by Saccardo, 1901 by Farlow, 1920 by Juel, and by many afterwards. Taking into account Fries's protologue for *Hyphelia terrestris*, this traditional interpretation is actually a misapplication of the name.

Juel (1920) observed that the macroscopical description of *Hyphelia terrestris* in Fries (1829) matched well the collection he made near Uppsala in 1916 and a similar collection made in Mustiala, Finland in 1865 by P.A. Karsten, who identified it as *Hyphelia terrestris* (UPS). Convinced that the observed conidiogenesis in these specimens had to be that of *Hyphelia terrestris*, Juel emended the genus *Hyphelia* (for the part regarding *Hyphelia terrestris*) adding “rami conidiophori, apice non inflati, conidiis rotundis brevissime pedicellatis undique tecti” to the Fries description.

Hennebert (1973) accepted Juel's interpretation of *Hyphelia terrestris* as a *Chromelosporium*-like species and interpreted (erroneously) Juel's publication as a lectotypification of *Hyphelia terrestris*. Actually Juel did not typify the name from any authentic Friesian material or from the two specimens that he cited. Hennebert named the fungus *Chromelosporium*

tuberculatum (Pers.) Hennebert, *Trichoderma tuberculatum* being the first synonym cited by Fries but for which no type exists. As *Hyphelia terrestris* had been sanctioned (Fries 1829), the name was corrected to *Chromelosporium terrestre* (Fr.) M.B. Ellis.

Fries (1825) originally introduced the generic name *Hyphelia* for *Trichoderma roseum* Pers. [= *Trichothecium* Link, fide Hughes 1958]. Fries (1825) also added “Aliud genus, mucedineum, representat vulgatissimum *Trichoderma tuberculatum* Pers. cui accedunt multae species novae.... Sed de his plura in S. M. III” [a reference to the forthcoming *Systema Mycologicum* 3]. “Huic generi *Trichodermatis* nomen tribuerem, nisi *T. viridi* jam a Cel. Linkio affixum, quod sancte servandum videtur.”

However, instead of creating his proposed new genus (‘aliud genus’), Fries (1829) actually divided *Hyphelia* into two unranked infrageneric parts: *Thelephoroideae* (for *H. rosea*, *H. spadicea*, *H. fusca*, and *H. nigrescens*) and *Hyphomycetoidea* (for the new species *H. terrestris*, described only macroscopically and with four synonyms).

Fries (1849) reduced his concept of *Hyphelia* by omitting the type, *H. rosea* (Pers.) Fr. and chose section names (instead of adjectives) for the subdivisions: *Xylohypha* for *H. nigrescens* and *H. fusca*; and *Geohypha* for *H. terrestris*. The omission of the type, *H. rosea*, made *Hyphelia* Fr. 1849 an illegitimate later homonym of *Hyphelia* Fr. 1825, nom. sanct. The names of the subdivisions *Geohypha* Fr. and *Xylohypha* Fr. are legitimate and available for elevation to generic rank.

Fries (1829) described *Hyphelia terrestris* only macroscopically, with four synonyms: “*Trichoderma tuberculatum* Pers.; *T. nemorosum* Pers.; *T. laeve* Schum. (dubitans ipse citat *T. laeve* Pers.); and *T. varium* Ehrenb.”

Searching for the type material of these names, I have been informed that no authentic specimen exists for *Hyphelia terrestris* in UPS or S, and no specimen of *Trichoderma tuberculatum* remains in L. Specimens of *Trichoderma laeve* and of *Trichoderma nemorosum* are preserved in L. and of *T. varium* in B and STR.

The examination of these authenticated specimens, one of *Trichoderma laeve*, (not the one labelled “*Trichoderma laeve?*” by Persoon), one of *T. nemorosum*, and three of *T. varium* revealed that they represent one species distinguished from *Chromelosporium*-like species by conidiogenesis.

Persoon (1796) describes *Trichoderma tuberculatum*, with ash grey conidia (“pulvere cinereo”), like the grayish conidia (“clair-cendré”) of *T. nemorosum*, suggesting that *T. tuberculatum* was similar to *T. nemorosum*.

Persoon also described the conidia of *T. laeve* as yellow, as Schumacher described his *T. laeve*. Ehrenberg described conidia of *T. varium* as variable in colour, while Fries described them as “subargillaceis”.

The other specimen, labelled ‘*Trichoderma laeve* ?’ by Persoon, contains pieces of young conidiogenous cells of a *Chromelosporium*-like fungus, differing from his other labelled ‘*Trichoderma laeve*,’ thus explaining Persoon’s question mark. Persoon’s doubt affected Fries (1829), who wrote “dubitans ipse citat *T. laeve* Pers.” and cited instead “*T. laeve* Schum. ! Saell. 2 p. 236”, a later homonym, of which Fries had seen a specimen. This illuminates the subsequent confusion between *Hyphelia terrestris* and the *Chromelosporium*-like fungi. This indicates also that the Friesian concept of *Hyphelia terrestris* differed from its traditional interpretation as a *Chromelosporium*-like fungus.

The most accurate interpretation of the nomenclature is to respect Fries’s 1829 protologue of *Hyphelia terrestris* (a sanctioned name) and lectotypify the species by one synonym, of which material exists—*Trichoderma varium* Ehrenb.—rather than *T. tuberculatum* Pers. and *T. laeve* Schumach., which lack extant material.

With the generic name *Hyphelia* 1849 being illegitimate as a later homonym, *Hyphelia terrestris* therefore has status of type species of *Geophypha* Fr. which can be raised in rank to a genus. A parallel nomenclatural interpretation was made for *Hyphelia nigrescens* (Pers.) Fr., now regarded as the type species of the genus *Xylohypha* (Fr.) E.W. Mason by Deighton (1960).

***Geophypha* (Fr.) Hennebert, stat. nov.**

MB 835628

≡ *Hyphelia* sect. *Geophypha* Fr., Summa Veg. Scand. 2: 447, 1849.

TYPE SPECIES: *Geophypha terrestris* (Fr.) Hennebert

= *Hyphelia* [unranked] *Hyphomycetoidea* Fr., Syst. Mycol. 3(1): 213, 1829, nom. sanct.

Ascomycota, ascomata unknown.

HYPHAE septate, hyaline, intricate, irregular, branched.

CONIDIOPHORES short as lateral outgrowths from vegetative hyphae bearing one conidium or long narrow sinuous and self-ramified branch, sparsely septate, bearing a conidium on each of the many lateral outgrowths and terminal ends.

CONIDIOGENESIS thallic, solitary on hyphal outgrowths, secession schizolytic.

CONIDIA one-celled, globose or subglobose, sometimes napiform, hyaline, smooth to verrucose.

HABITAT on soil.

***Geohypha terrestris* (Fr.) Hennebert, comb. nov.**

FIGS 22, 23

MB 835629

- ≡ *Hyphelia terrestris* Fr., Syst. Mycol. 3(1): 213, 1829, nom. sanct.
- ≡ *Ostracoderma terrestre* (Fr.) Nannf., Fungi. Exsicc. Suec., Fasc. 53–54, Schedae: 40, 1959.
- ≡ *Chromelosporium terrestre* (Fr.) M.B. Ellis, More Demat. Hyphom.: 154, 1976.
- = *Trichoderma tuberculatum* Pers., Ann. Bot. (Usteri) 15: 12, 1795 [as “*tuberculata*”].
- ≡ *Chromelosporium tuberculatum* (Pers.) Hennebert, Persoonia 7: 198, 1973.
- = *Trichoderma laeve* Pers., Observ. Mycol. 1: 12, 1796.
- = *Trichoderma varium* Ehrenb., Sylv. Mycol. Berol.: 22, 1803.
- = *Trichoderma nemorosum* Pers., Traité Champ. Comest.: 131, 1818.
- = *Botrytis ceratioides* Peck, Annual Rep. New York State Mus. Nat. Hist. 35: 139, 1884.
- = *Sporotrichum fossarum* Fautrey, Rev. Mycol. (Toulouse) 17: 71, 1893.
- ≡ *Ostracoderma fossarum* (Fautrey) S. Hughes, Canad. J. Bot. 36: 792, 1958.

TYPE: *Trichoderma laeve* Pers.? [*laeve* Pers.? scratched off] *varium* m. [mei] ad Berol. in terra umbrosa humida, Thg. [Thiergarten] Berlin, 7/8 [Aug. 7] [scr. Erhenberg]. Herb. Ehrenberg (B, MBT 392413, here designated as lectotype; isolectotypes: [DAOM 83392, DAOM 83393, MUCL 2387, MUCL 2388]).

COLONIES in small cushions, around 5 mm across, linked by a web-like mycelium, greyish yellow when fresh, brown when dried.

HYPHAE narrow, irregular in diameter, 2–4 µm, sometimes inflated to 6 µm before septa and constricted at septa, hyaline, thin-walled, with abundant lateral narrower branchlets, fertile.

CONIDIOGENUS CELLS either reduced to a conical to cylindrical lateral outgrowth of the hypha, 2–8 × 1–1.5 µm or (most often) developed into a long and narrow, sinuous, irregular, hypha, 8–50 × 1–1.5 µm, possibly ramified, producing ≤15–20 thallic conidia on lateral outgrowths and terminal ends.

CONIDIA thallic, solitary, borne on each hyphal outgrowth, seceding schizolytically through a 1–1.5 µm wide septum, one-celled, globose or subglobose, 4.5–6(–6.5) µm, hyaline, with a thick wall, at first smooth, soon becoming verrucose, with 12–15 warts in median view.

HABITAT: on bare soil after rain in forest.

COMMENTS—The type and authentic specimens of the species cited in the nomenclator are microscopically characterized as having narrow, sinuous conidiogenous hyphae and verrucose conidia mixed with young smooth conidia, the relative abundance depending on maturity of the fungus.

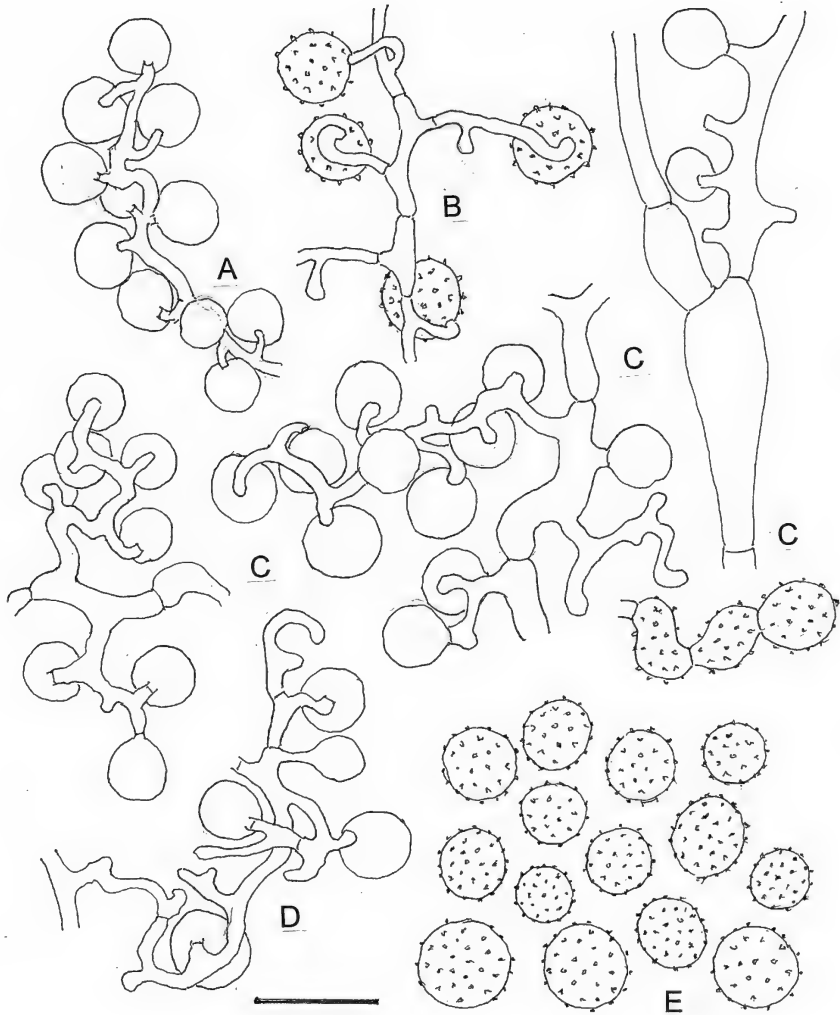


Fig. 22. *Geohypha terrestris*. A. *Trichoderma laeve* (MUCL 2462) conidiogenous cell with young conidia. B. *Trichoderma varium* (lectotype, MUCL 2387) with mature conidia. C. *Sporotrichum fossarum* (holotype, MUCL 2486b and isotype, MUCL 2394), conidia borne either solitary on hyphae, or numerous on tortuous conidiogenous hyphae. D. *Botrytis ceratioides* (holotype, MUCL 2467) conidiogenous cell, after release of some conidia. E. Mature conidia from these four specimens. Scale bar = 10 µm.

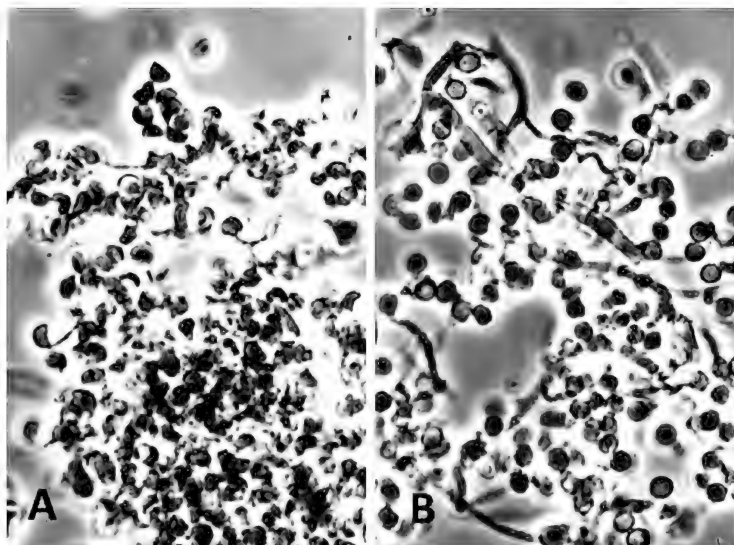


Fig. 23. A *Trichoderma laeve* Pers. (MUCL 2387). B. *Trichoderma varium* Ehrenb. (MUCL 2387) (Photos made by J.W. Carmichael, University of Alberta Mold Herbarium in 1961).

The size of the conidia obtained from each specimen drawn in Fig. 21 are *T. laeve* 4.5–5.5 (av. 5) μm , *T. varium* 4–6 (av. 5) μm , *B. ceratioides* 5–6(–6.8) (av. 5.7) μm , and *S. fossarum* 4–6.5 (av. 5) μm .

In 1961, I sent slides of *Trichoderma laeve* and *T. varium* from Persoon's herbarium to J.W. Carmichael for comparison with *Chrysosporium* species. He responded with photographs of the slides, and the opinion that the species were not congeneric with *Chrysosporium*.

The type of *Sporotrichum fossarum* contains two packets, one wrapped in paper contains soil in powder form on a piece of blotting paper (MUCL 2486a) and the other, in an aluminium sheet, contains the same soil kept compact and bearing the fungus (MUCL 2486b). The same fungus was distributed in G. Roumeguère's Fungi Selecti Exsiccati 6790 (MUCL 2394). The fungus has abundant vegetative hyphae that are often inflated before the septa and, when mature, verrucose conidia. Seeing the similarities with an *Ostracoderma* sp. sensu Juel, Hughes (1958) classified the species as *Ostracoderma fossarum*. Hennebert (1973) made it a synonym of *Chromelosporium tuberculatum*, an opinion later reported by Stalpers (1984). Revisiting the collection, I now assert that *Sporotrichum fossarum* is neither an *Ostracoderma* nor a *Chromelosporium* species but what is identified here as *Geohypha terrestris*.

SPECIMENS EXAMINED

TYPE & AUTHENTIC SPECIMENS: **EUROPE**: (3) *Trichoderma laeve* [scr. Persoon] Herb. Persoon (L 910.264.459) [MUCL 2462] (not L 910.264. 31, *Trichoderma laeve*? as written by Persoon). (4) *Trichoderma nemorosum* [scr. Persoon] Herb. Persoon (L 910.264-) [DAOM 83900, MUCL 2463]. (5) *Trichoderma varium* Ehb. orig. [on soil] [scr. Ehrenberg] Herb. Schwaegrichen [stamped]” (STR) [DAOM 83898, MUCL 2441]. (6) “*Trichoderma varium* Ehrenb. [on soil, no locality, no date] [scr. Ehrenberg] (B) (DAOM 83394, MUCL 2389). **FRANCE** (7). *Sporotrichum fossarum* sp.n. Fautrey, sur la terre déjetée des fossés dans les bois humides. La Forêt de Clamecy. Été 1894, Fautrey 212 (holotype) (UPS) [DAOM 83912, MUCL 2486-a, 2486-b]. (8) *Sporotrichum fossarum* n. sp. Fautrey, sur la terre rejetée des fossés dans les bois humides, été 1894. F. Fautrey (isotype). G. Roumeguère Fungi Selecti Exsiccati 6790 (Rev. Myc. 1895, p. 71, n.49) (G, NY) [MUCL 2394]. **GERMANY** (9) *Botrytis epigaea* Link, [var. *alba*] ad terram humidam, non raro, Aestate. Fuckel. Fungi Rhenani Fasc. II, 1863, n° 147 (BX 47111, GRO, S, K, FH) [MUCL 1798]. (Jahrb. Nassauischen Vereins. Naturk. 23: 363. 1870, p. 363 as, *Hyphelia terrestris* Fr. var. *alba*, nom. inval.). **USA**: **NEW YORK** (10) *Botrytis ceratioides* Peck, on decaying wood of *Tsuga canadensis*, Albany, June, leg. C.H. Peck. (holotype). See 35th Report p.139, 1884 (NYS) [MUCL 2467].

OTHER SPECIMENS: **EUROPE**: **ITALY** (11) *Botrytis epigaea* Lk. f. *cinerea*, ad terram argillosam udam, Bosco Montello (Treviso), Sept. 1875. Saccardo Mycotheca Veneta 58 (K-M) [MUCL 2295]. **FRANCE** (12) *Trichoderma nemorosum* Pers. Autumno, ad terram, St Cloud, near Paris. Herb. de Candolle (G 005431) [DAOM 83992, MUCL 2392]. (13) *Trichoderma nemorosum* Pers. [on soil] Meudon, Augusto [no year] Herbier Lévillé in Herb. de Candolle (G 005432) [DAOM 83899, MUCL 2393]. **SWEDEN** (14) *Hyphelia*, on half buried birch branches in *Sphagnum* cushion, Gästrikland, NNW of Tolfors Swampy wood, Aug. 14 1950, J.A. Nannfeldt. Flora Suecica 11057 (UPS) [MUCL 2479a]. **NETHERLANDS** (15) *Hyphelia terrestris* Fr. in terra argillacea, Lugd. Batava, 1844, Oudemans (GRO) [MUCL 2775]. **DENMARK** (16) *Hyphelia terrestris* Fr. on bare soil, Saelland, Tisvilde Heg., Oct. 4 1955, J.A. Nannfeldt. Flora Danica 14249 (UPS) [DAOM 84938a, MUCL 2495]. **BELGIUM** (17) *Trichoderma laeve* on bare soil, Lauzelle forest, Ottignies-LLN, Oct. 2017, G.L.H. (MUCL 56656).

NORTH AMERICA: **USA**: **NEBRASKA** (18) *Botrytis ceratioides* Peck [on leaves and mosses] Lincoln, 1200 ft, July 22 1890, T.A. Williams. Nebraska Flora 312 (BP) [MUCL 2423]. **CANADA**: **ONTARIO** (19) *Rhinotrichum carneum* Ell. & Ev. on dead wood, Oct. 3 1896, Macoun, Ellis collection 185. (NY) [MUCL 2838]. (20) *Trichoderma laeve* Pers. on soil, Queen’s University Biological Station, near Chafey’s Lake, Ontario, July 12 1961, det. G.L. Hennebert (MUCL 2537).

Plicaria endocarpoides

Hennebert (1973) suggested that *Plicaria endocarpoides* could have a *Chromelosporium*-like asexual morph in culture based on a strain from J.W. Paden. The strain DAOMC 199565 produced on malt agar a conidial state having no similarity with *Chromelosporium* as illustrated here.

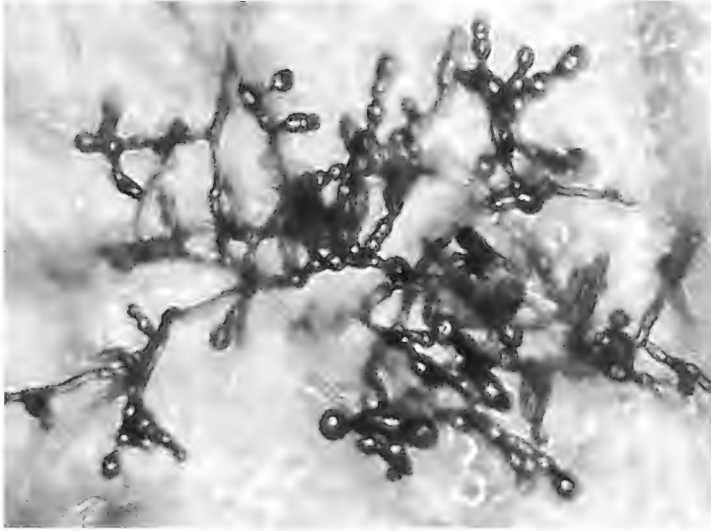


Fig. 24. *Plicaria endocarpoides* (DAOMC 199565 = MUCL 57202).
Conidial morph on malt-agar.

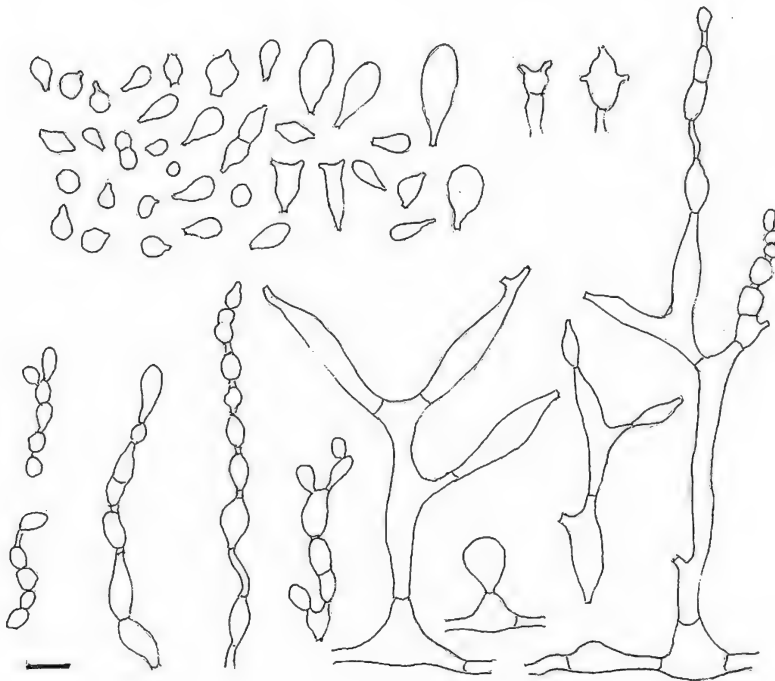


Fig. 25. *Plicaria endocarpoides* (DAOMC 199565 = MUCL 57202).
A. Conidiophores and conidia on malt agar. Scale bar = 10 μ m.

Plicaria endocarpoides (Berk.) Rifai, Verh. Kon. Ned. Akad. Wetensch., Afd.

Natuurk., Sect. 2, 57(3): 255, 1968.

FIGS 24, 25

≡ *Peziza endocarpoides* Berk., in Hooker, Fl. Nov.-Zel. 2: 199, 1855.

MYCELIUM hyaline prostrate on malt agar.

CONIDIOPHORES erect from creeping hyphae, one or pluri-celled, 10–110 µm high, the basal cell enlarged, triangular, the stipe often furcate.

CONIDIOGENUS CELLS intercalary or terminal of the conidiophore, cylindrical, fusiform, or triangular, 5–8 µm wide, producing acropetal solitary or branched chains of conidia, leaving unthickened scars at schizolytic secession.

CONIDIA hyaline, smooth, one-celled, some 2–3-celled, variable in shape, from globose (3–5 µm), to ovate, pyriform, or citriform (5–23 × 3–8 µm), most one celled, some septate, ramoconidia bearing one to three scars of attachment of simple or branched chains of conidia.

SPECIMENS EXAMINED: CANADA: BRITISH COLUMBIA. *Plicaria endocarpoides* (Berk.) Rifai, on burnt wood, slash and ash in coniferous forest, Lightning Lakes trail, Manning Provincial Park, British Columbia, June 9 1985, K.N. Egger 2044 in living culture (CCF 6892 = DAOMC 199565 = MUCL 57202).

Conclusion

In light of certain mononematous *Chromelosporium* asexual morphs actually representing *Peziza* or *Plicaria*, and certain synnematos *Chromelosporiopsis* asexual morphs representing *Pachyphloides*, it was logical to emphasize a morphological character to distinguish the asexual morphs of these *Pezizaceae*. The chosen criterion of conidiophore fasciculation allows segregating similar conidial fungi not known to have sexual morphs into two genera—*Chromelosporium* around its mononematous type and the new genus *Chromelosporiopsis* for the synnematos species. *Chromelosporium* includes here five taxa with distinct morphologies. *Chromelosporiopsis* comprises so far two named taxa. In addition to the excluded taxa, there remain some doubtful taxa showing some (but insufficient) *Chromelosporiopsis* and a set of unidentified species detected among the herbarium specimens that further morphological investigation of might allow segregation into species. It is recommended that any new fresh conidial samples be not only genetically analysed but accurately described in their finest morphological details (including electron microscopy) to allow characterization and identification of these conidial fungi, many of which are likely to be asexual morphs of some known *Pezizaceae*.

Examination of many herbarium specimens revealed a long history of misapplication of the name *Hyphelia terrestris*, irrespective of Fries protologue of the species. A neotype of the species designated among the synonyms given by Fries allowed a new description of the species renamed *Geohypha terrestris*.

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I am thankful to my colleagues, Dr. Keith Seifert (Adjunct Professor, Carleton University, Ottawa and formerly of Ottawa Research and Development Center, Agriculture and Agri-Food Canada) and Dr. David L. Hawksworth (Royal Botanic Gardens Kew), who thoroughly and accurately revised the manuscript in agreement with the present rules of nomenclature. I thank Dr Scott Redhead (Curator, National Mycological Herbarium (DAOM), Agriculture and Agri-Food Canada) for his appreciated nomenclatural advice and Dr Konstanze Bensch, (Mycobank curator, Westerdijk Fungal Biodiversity Institute, Utrecht) for the registration of names and types in Mycobank and her meticulous revision of all name citations. I thank Dr M. Scherrenberg and Dr J. Nuytinck of Naturalis Biodiversity Center in Leiden for the photographs and examination of the precious Persoon's material of *Isaria carnea* and Mr Jonathan Mack from Quebec for the photographs of *Chromelosporium coeruleascens* I thank also Dr Shaun Pennycook and Dr Lorelei Norvell, editors of Mycotaxon, for editing the paper through very friendly exchanges. Also I remain grateful to the late Dr R.P. Korf of Cornell University, Ithaca, for his profound friendship and the multiple scientific exchanges and support for this research, particularly during 1973.

A personal note of gratitude to late Dr. Stanley J. Hughes

I am overall deeply grateful to late Dr. Stanley J. Hughes, a great mycologist, who was a great teacher and a loyal friend. After sending him some pages of my doctoral thesis on the genus *Botrytis*, inspired by some of his major publications, I received an invitation to apply for a National Research Council of Canada postdoctoral fellowship in the Mycology Section of the then Plant Research Institute of the Department of Agriculture Canada, in Ottawa, from October 1960.

My wife Lidwina and I arrived in Canada at the end of September 1960 and were received by Stanley and Lyndell Hughes. Once we were settled in the apartment they had carefully prepared for us, Stan introduced us to his colleagues of the Mycology Section in the Neatby Building at the Central Experimental Farm. The following day, Stan immediately began my training with a collecting trip to Gatineau Park near Ottawa (Fig. 26).

In the laboratory, showing great patience and efficiency with the student I then was (speaking only a few words of English accented French), Stan tested my skills with a simple project, describing *Balanium* from the DAOM herbarium. Then followed the description of *Arachnophora fagicola*, a new genus and species collected



in Belgium. As many as seven times, he asked me to improve the manuscripts I submitted to him, each word having to be useful and necessary.

To introduce me to ancient mycological literature, Stan asked me to clarify the complex history of *Oedemium didymum*. To describe the apothecial stage of certain *Botrytis* species reported in my doctoral thesis, Dr. J.W. Groves, in charge of the Mycology Section, with Dr. Elliot, introduced me to the in vitro production of the apothecia of *Botrytis* from living strains.



During the second year of the award, Stan (FIG. 27A) urged me to develop my research on the *Botrytis*-like fungi begun in my PhD thesis and which he classified in *Ostracoderma*. In 1973, incited by Dr Korf to publish, I revised some *Botrytis*-like genera and renamed *Ostracoderma* species in *Chromelosporium* (also described and illustrated in the present paper).

Those two years of mycological training with Dr. Hughes and Dr. Groves not only were essential to my career, but also provided the opportunity for creating an indestructible bond of respect and friendship. Later, Stan Hughes did to me the honour of visiting my laboratory at the UCL in Herverlee-Leuven in May 1973 (FIG. 27B) and in Louvain-la-Neuve in June 1994 (FIG. 27C) at the celebration of the Centenary of the MUCL fungus collection (Hennebert 2010). I remain very grateful to the late Stanley J. Hughes for the quality of my training and his friendship.

Literature cited

- Bonorden HF. 1851. Handbuch der allgemeinen Mykologie als Anleitung zum Studium derselben. Stuttgart.
- Corda ACJ. 1837. Icones Fungorum hucusque cognitorum, Part 1, Prague.
- Ellis MB. 1976. More dematiaceous Hyphomycetes. Kew, Commonwealth Agricultural Bureau.
- Fresenius G. 1852. Beiträge zur Mykologie, Heft 2: 39–89. Frankfurt.
<https://doi.org/10.5962/bhl.title.51534>
- Fries EM. 1825. Systema Orbis vegetabilium, I. Plantae hormonemae. Lund.
- Fries EM. 1829. Systema mycologicum, Vol. 3(1). Gryphiswald.
- Fries EM. 1832a. Systema mycologicum, Vol.3(2). Gryphiswald.
- Fries EM. 1832b. Index alphabeticus generum, specierum et synonymorum in Eliae Fries Systemate mycologico ejusque Supplemento 'Elencho Fungorum' enumeratorum. Gryphiswald.
- Fries EM. 1849. Summa vegetabilium Scandinaviae. Vol. 2, Stockholm.
- Fuckel L. 1870. Symbolae mycologicae. Jahrbücher des Nassauischen Vereins für Naturkunde 23–24. 459 p.
- Healy RA, Hobart C, Tocci GE, Bónar L, Merenyi Z, Paz Conde A, Smith ME. 2015. Fun with the discomycetes: revisiting collections of Korf's anamorphic *Pezizales* and Thaxter's New England truffles leads to a connection between forms and the description of two new truffle species: *Pachyphlodes pfisteri* and *P. nemoralis*. *Ascomycetes.org*. 7(6): 357–366.
<https://ascomycete.org/Portals/0/Archives/AscomyceteOrg%2007-06%20357-366.pdf>
- Healy R, Pfister DH, Rossmann AY, Marvanová L. 2016. Competing sexual-asexual generic names of *Pezizomycetes* and recommendations for use. *IMA Fungus* 7: 285–288.
<https://doi.org/10.5598/imafungus.2016.07.02.08>
- Hennebert GL. 1960. Recherches morphologiques sur le genre *Botrytis* Persoon. PhD thesis – UCL, Louvain. 187 p.
- Hennebert GL. 1973. *Botrytis* and *Botrytis*-like genera. *Persoonia* 7(2): 183–204.
- Hennebert GL. 2017. *Glischroderma* Fuckel. *Mycotaxon* 132: 745–757.
<https://doi.org/10.5248/132.745>
- Hennebert GL. 2010. The 100 years of the Fungus Collection MUCL 1894–1994. Fungal taxonomy and tropical mycology, Quo vadis? Taxonomy and nomenclature of the fungi. Louvain-la-Neuve. <https://doi.org/10.5248/2010mucl.pdf>
- Hennebert GL, Decock C. 2020. A comparison of anamorphs of some *Pachyphlodes* species and the type of *Chromelosporium*: Are they congeneric? *Mycotaxon* 135(1): 167–182.
<https://doi.org/10.5248/135.167>

- Hennebert GL, Korf RP. 1975. The peat mould, *Chromelosporium ollare*, conidial state of *Peziza ostracoderma*, and its misapplied names, *Botrytis crystallina*, *Botrytis spectabilis*, *Ostracoderma epigaeum* and *Peziza atrovinosa*. *Mycologia* 67(2): 214–240. <https://doi.org/10.2307/3758415>
- Hodge K. 2017. *Chromelosporium coerulescens*, photos. /blog.mycology.cornell.edu. Also www.facebook.com/pg/CornellFungi/photos/?tab=album&album_id=1637053939892411/
- Hughes SJ. 1958. Revisiones Hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canadian Journal of Botany* 36: 727–836. <https://doi.org/10.1139/b58-067>
- Jaklitsch W, Baral HO, Lücking R, Lumsch HT. 2016. Syllabus of Plant Families. Adolf Engler's Syllabus der Pflanzenfamilien. 13th ed. Part 1(2) *Ascomycota*. Borntraeger Science Publishers, Stuttgart. <https://doi.org/10.13158/heia.29.1.2016.207>
- Juel HO. 1920. Über *Hyphelia* und *Ostracoderma*, zwei von Fries aufgestellte Pilzgattungen. *Svensk Botanisk Tidskrift* 14: 212–222.
- Kirk PM, Cannon P, Minter D, Stalpers J. 2008. Ainsworth and Bisby's dictionary of the Fungi, 10th ed. CABI, Wallingford. <https://doi.org/10.1079/9780851998268.0000>
- Korf RP. 1994. Fifty years of fun with the discomycetes and what's left to do. Opening lecture of the First Whetzel-Wescott-Dimock Lectureship, Cornell Univ., Ithaca.
- Labbé R. 2015. *Chromelosporium coerulescens*, taxon IUMQ254. /mycoquebec.org/
- Persoon CH. 1795. Observationes mycologicae. *Annalen der Botanik (Usteri)* 15: 1–39.
- Persoon CH. 1796. Observationes mycologicae, pars prima. Leipzig. 116 p.
- Preuss CGT. 1853. Uebersicht unterzogter Pilze, besonders aus der Umbeugend von Hoyerswerda, *Linnaea* 26: 705–725.
- Saccardo PA. 1881. Fungi italici autographice delineati, tab. 641–1120. Padova.
- Saccardo PA. 1886. Sylloge hyphomycetum. Sylloge Fungorum 4. Padova. 807 p.
- Saccardo PA. 1877. Fungi veneti novi vel critici. Ser. VI. *Michelia* 1: 1–72.
- Schweinitz LD von. 1832. Synopsis fungorum in America boreali media degentium. *Transactions of the American Philosophical Society*, ns 4: 141–316. <https://doi.org/10.2307/1004834>
- Seifert K, Morgan-Jones G, Gams W, Kendrick B. 2012. The genera of hyphomycetes. CBS Biodiversity Series 9. 997 p.
- Stalpers JA. 1984. A revision of the genus *Sporotrichum*. *Studies in Mycology* 24. 105 p.
- Sumstine DR. 1911. Studies in North American hyphomycetes—I. The genera *Rhinotrichum* and *Olptrichum*. *Mycologia* 3: 45–56. <https://doi.org/10.1080/00275514.1911.12017662>
- Wijayawardene NN, Hyde KD, Al-Ani LKT, Tedersoo L, Haelewaters D, Rajeshkumar KC, Zhao RL, Aptroot A, & al. 2020. Outline of Fungi and fungus-like taxa. *Mycosphere* 11(1): 1060–1456. <https://doi.org/10.5943/mycosphere/11/1/8>